



SeaWiFS Technical Report Series

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Volume 42, Satellite Primary Productivity Data and Algorithm Development: A Science Plan for Mission to Planet Earth

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PREFACE

The scope of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Project encompasses a broad variety of topics, as evidenced by the myriad subjects covered in the *SeaWiFS Technical Report Series*. Each of the so-called *case studies* volumes, as well as the calibration topic volumes, contain several chapters discussing topics germane to the subject of calibration and validation. In a departure from this, Volume 42, discusses topics germane to the issue of primary productivity—a critical part of the SeaWiFS Project. This volume further demonstrates both the breadth and complexity of the issues that the Project must address, and provides further justification for primary productivity research.

The chapters in this volume present discussions regarding:

- a) The use of satellite data to derive primary productivity in the world ocean; and
- b) The progress made toward a consensus productivity algorithm for SeaWiFS.

Greenbelt, Maryland
September 1997

— C. R. McClain

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ABSTRACT

Two issues regarding primary productivity, as it pertains to the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Project and the National Aeronautics and Space Administration (NASA) Mission to Planet Earth (MTPE) are presented in this volume. Chapter 1 describes the development of a science plan for deriving primary production for the world ocean using satellite measurements by the Ocean Primary Productivity Working Group (OPPWG). Chapter 2 presents discussions by the same group of algorithm classification, algorithm parameterization and data availability, algorithm testing and validation, and the benefits of a consensus primary productivity algorithm.

Prologue

The purposes of the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Project is to obtain valid ocean color data of the world ocean for a five-year period, to process that data in conjunction with ancillary data to meaningful biological parameters, and to make that data readily available to researchers. The National Aeronautics and Space Administration (NASA) Goddard Space Flight Center (GSFC) developed a data processing and archiving system in conjunction with the Earth Observing System Data and Information System (EOSDIS), which includes a ground receiving system.

SeaWiFS is a follow-on sensor to the Coastal Zone Color Scanner (CZCS), which operated aboard NASA's Nimbus-7 satellite from 1978–1986. CZCS started as a one year proof-of-concept mission to determine if satellite sensors could, in fact, detect ocean color from space. Surprisingly, the instrument was operational for a full eight years, instead of the anticipated one year. SeaWiFS improves on CZCS by giving global coverage every 48 hours (which CZCS was not capable of doing at all), by giving an improved atmospheric correction scheme, and by giving a more accurate determination of phytoplankton concentration. How fast this concentration changes with time and/or how much photosynthesis is going on during the course of a day is called "primary productivity." It is called *primary* productivity because it is the critical, initial step in the food chain. In order to understand the productivity of the ocean, scientists must first be able to estimate it. Using algorithms designed for satellite ocean color data, they can then verify the derived product (e.g., primary productivity, chlorophyll, or geophysical parameters) using field measurements.

Because many of the studies and other works undertaken with the SeaWiFS Project are not extensive enough to require dedicated volumes of the *SeaWiFS Technical Report Series*, the SeaWiFS Project, in collaboration with the *Series'* editors, decided to publish volumes composed of brief, but topically specific, chapters. This volume presents two related discussions on the subject of primary productivity. A short synopsis of each chapter in this volume is given below.

1. *Using Satellite Data to Derive Primary Productivity in the World Ocean*

In January 1994, NASA sponsored the first meeting of the Ocean Primary Productivity Working Group (OPPWG) at Brookhaven National Laboratory. Over the next 18 months, two other workshops were held, the latest of which was held at GSFC in Greenbelt, Maryland, on 11–13 June 1996. Thirty-nine participants representing several different countries, including Taiwan, Japan, France, Norway, and Canada attended the meeting at GSFC. The major goal of the workshop was the development of a science plan for deriving primary production for the world ocean from satellite measurements. Results of the workshop are presented here. This science plan presents a set of consensus recommendations from the scientific community which are designed to help guide NASA's Mission to Planet Earth (MTPE) programs to use US and international assets as constructively and productively as possible to achieve its goals.

2. *Toward a Consensus Productivity Algorithm for SeaWiFS*

An OPPWG was formed to discuss the benefits and fundamental problems associated with using SeaWiFS and other ocean color satellite measurements for estimating oceanic primary production. During the first, and subsequent, OPPWG meetings, discussions focused on: 1) algorithm classification, including similarities and differences between currently available productivity algorithms; 2) algorithm parameterization and data availability; 3) algorithm testing and validation; and 4) the concept and benefits of a consensus SeaWiFS productivity algorithm. The productivity algorithms discussed range from simple statistical (empirical) relationships between surface chlorophyll concentration and photosynthesis, to complex theoretical models which derive time- and depth-specific photosynthetic rates from spectral models of irradiance distributions and depth-dependent chlorophyll distributions. Each classification of productivity algorithms has benefits and drawbacks. This report describes the results from the first OPPWG meeting and the scientific issues involved with developing a consensus SeaWiFS productivity algorithm.

Chapter 1

Using Satellite Data to Derive Primary Productivity in the World Ocean

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ABSTRACT

In January 1994, NASA sponsored the first meeting of the OPPWG at Brookhaven National Laboratory. Over the next 18 months, two other workshops were held, the latest of which was held at GSFC in Greenbelt, Maryland, on 11–13 June 1996. Thirty-nine participants representing several different countries, including Taiwan, Japan, France, Norway, and Canada attended the meeting at GSFC. The major goal of the workshop was the development of a science plan for deriving primary production for the world ocean from satellite measurements. Results of the workshop are presented here. This science plan presents a set of consensus recommendations from the scientific community which are designed to help guide NASA's MTPE programs to use US and international assets as constructively and productively as possible to achieve its goals.

1.1 INTRODUCTION

The estimation of primary productivity from satellite measurements of ocean color is critical for developing an understanding of how ocean biological processes affect, and are affected by, changes in atmospheric radiative budgets and global biogeochemical cycles. Up until now, however, the derivation of primary productivity has been treated by NASA as an ad hoc activity of the research community. Inevitably, different research groups have developed different models and published different model output. It has been difficult to establish whether differences in model output are a consequence of parameterization schemes, model structure, algorithm code, or other factors.

In 1994, the international ocean sciences community established, under the sponsorship of the SeaWiFS Program, an OPPWG† to help evaluate the variations and similarities between the myriad models. This report, developed by the OPPWG, provides guidance for developing a traceable, operational algorithm that can be used with any ocean color data which derive upper ocean pigment fields. Algorithm performance will be evaluated from independent, single-blind, round-robin exercises using standardized data files.

Recommendation: It is recommended that NASA, in collaboration with the Joint Global Ocean Flux Study

(JGOFS), develop or establish an openly accessible database in *in situ* measurements for primary production algorithm parameterization.

The database should be linked to JGOFS and other complementary field programs. The latter should include seasonal and interannual atmospheric gas measurements. The science plan calls for an understanding of the underlying causes of variation in the quantum yields in the world ocean, with the goal of developing prognostic models to predict biological responses within a given set of physical and biogeochemical scenarios.

Implementation of the algorithm code will be dual-tracked, using both the SeaWiFS Project and the Moderate Resolution Imaging Spectroradiometer (MODIS) Instrument Team, and the Earth Observing System (EOS) Product Generation System (PGS) within EOS. Quality assurance of remotely sensed data will be provided through the Sensor Intercomparison and Merger for Biological and Interdisciplinary Oceanic Studies (SIMBIOS) Project and the international ocean sciences community. The initial results of the effort will be the establishment of a standard productivity product within two years following the launch of SeaWiFS and iterative code development following on as a template for all ocean color sensors into the 21st century.

1.2 LIFE ON EARTH

A fundamental objective of the MTPE is to develop observational tools necessary for understanding the regu-

† P. Falkowski is the lead author of this chapter, however, it was written with input from the entire OPPWG, whose names appear in the list of Participants, Appendix A.

Table 1. Comparison of productivity and biomass in marine and terrestrial ecosystems.

| Ecosystem Type | Total Net Primary Productivity [10^{15} g/yr] | Total Living Plant Biomass [10^{15} g] | Turnover Time [years] |
|----------------|--|---|-----------------------|
| Marine | 25–50 | 1–2 | 0.02–0.08 |
| Terrestrial | 50–75 | 600–800 | 8–16 |

lation and feedback of critical biogeochemical cycles, with the long-range goal of distinguishing between natural variations and anthropogenic influences thereon. This objective is essential to the successful development of coupled climate and biogeochemical models required for predicting climatic forcings and responses. A critical component of this mission is to develop the ability to quantify and understand factors controlling greenhouse gases, especially carbon dioxide, on both annual and decadal time scales.

In the modern biogeochemical epoch of Earth, the global carbon cycle is not in balance. Net oxidation of organic carbon, resulting primarily from the combustion of fossil fuels, exceeds net carbon fixation by the ensemble of photosynthetic organisms (Houghton et al. 1990). The consequences of an imbalanced carbon cycle on biological feedbacks and climate remain unclear. What is certain, however, is that the rate and magnitude of changes in the atmospheric composition of radiatively interactive atmospheric gases are unprecedented in the recent geological past (Sarmiento and Bender 1994). Primary net sinks for atmospheric CO_2 include chemical and physical sequestration in the ocean and photosynthetically-mediated biological sequestration and deposition. Of these processes, by far the most quantitatively uncertain is the biologically-mediated flux.

Photosynthetic processes occur in both oceanic and terrestrial ecosystems. The approximate magnitude of net carbon fixation and biomass in the two environments is known within approximately a 30% uncertainty (Table 1). It is clear from comparing the two ecosystems that:

1. The absolute magnitude of carbon fixation attributed to marine photosynthetic organisms accounts for approximately 40% of the global total;
2. Oceanic photosynthetic organisms turn over much more rapidly than their terrestrial counterparts; and
3. Marine photosynthetic organisms, composed almost entirely of single-celled phytoplankton, account for less than 1% of the total global plant biomass.

Thus, oceanic photosynthetic organisms are extremely efficient in fixing carbon compared to terrestrial plants, and they mediate a large flux of organic carbon into the ocean interior. This carbon flux sustains a steady-state, air-sea gradient in inorganic carbon and is often referred to as the *biological pump* (Volk and Hoffert 1985).

In models of the global carbon cycle used for constraining atmospheric gas measurements, the biological pump is commonly assumed to be in a steady state, however,

this assumption is clearly invalid on geological time scales. During glacial–interglacial cycles, there appear to be pronounced changes in the efficiency of the biological pump. These changes are inferred from the sedimentary record (Imbrie et al. 1992); the resultant changes in the ocean carbon cycle are inversely correlated with atmospheric CO_2 concentrations (Fig. 1 in this paper, taken from Sarmiento and Bender 1994). The factors leading to alterations in the biological pump, however, remain to be elucidated.

Major questions concerning the role of the oceanic biological CO_2 pump in the global climate are:

- a. Is the biological pump changing or is it in steady state?
- b. If it is changing, what is the sign of the change (i.e., positive or negative), and how will the change affect atmospheric gas composition?
- c. What could cause the biological pump to change and what is the capacity of the ocean to remove or add CO_2 from, or to, the atmosphere via biological processes?

These critical questions can be addressed only through a combination of long-term global remote sensing platforms, *in situ* measurements, and dynamic modeling of primary production and the carbon cycle in the world ocean.

1.2.1 Phytoplankton Diversity

There are approximately 1,500 species of prokaryotic and 28,500 species of eukaryotic aquatic photosynthetic organisms extant on Earth. Together, these organisms comprise approximately 18 phyla† and the ensemble is, in the vernacular, called algae (from the Latin for seaweed), the vast majority of which are phytoplankton. For comparison, all terrestrial plants evolved from a single class (Charophyceae) of a single phylum (Chlorophyta) of the algae. Thus, although there are approximately 240,000 species of higher plants, the genetic diversity represented by higher plants is small compared to algae. Algal diversity determines the structure of marine ecosystems and is critically important to the sustainable commercial exploitation of living marine resources.

† For illustrative purposes, it is interesting to consider that humans, chickens, and dinosaurs are all in the phylum Chordata; hence, the genetic distances that have emerged in the formation of 18 algal phyla are considerable.

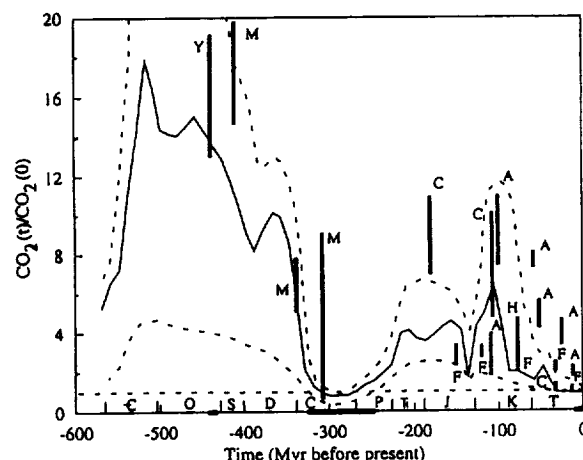


Fig. 1. The ratio of Phanerozoic atmospheric carbon dioxide to the present level plotted versus time in millions of years (Myr) (Berner 1992). The solid line and dashed uncertainty lines are from the theoretical model of Berner (1991). The horizontal bars along the abscissa indicate periods of glaciation, which coincide with low CO_2 levels except during the late Ordovician. The vertical bars are various estimates of paleo- CO_2 levels [Y=Yapp (1992); M=Mora et al. (1991); C=Cerling (1991); F=Freeman and Hayes (1992); A=Arthur et al. (1991); H=Hollander and McKenzie (1991)]. This figure is being reprinted here with kind permission from Kluwer Academic Publishers: from Sarmiento and Bender 1994, page 211, Fig. 2.

The diversity of phytoplankton affects photosynthetic processes (Appendix B) directly and indirectly. Direct effects are related to the optical absorption properties of the cells. An often used taxonomic screen for diversity is based on pigmentation. The pigment composition is qualitatively determined at the phylum level and, in some cases, provides a spectral signature that can be remotely detected. The quantum yield of photosynthesis is directly dependent on the efficiency of energy transfer from various pigments to the photosynthetic reaction centers.

Biological diversity is an indirect response to environmental changes. Ocean physics and chemistry change on daily, seasonal, annual, and climatological time scales, and affect the depth of mixing (and hence, the light regime), nutrient concentration, and temperature. In turn, each of these variables affects enzymatically catalyzed rates, optical absorption properties of cells, and synthesis of components in the photosynthetic apparatus. The ensemble of effects influences the achievable quantum yield for photosynthetic carbon fixation and, therefore, the efficiency of the biological pump.

1.2.2 Photosynthetic Processes

Regardless of the biological diversity represented in phytoplankton, the biophysical and biochemical processes responsible for basic photosynthetic reactions are extraordinarily conserved. All oxygenic phytoplankton contain

chlorophyll *a* in their reaction centers (with the exception of marine prochlorophytes which have the slightly modified derivative divinyl chlorophyll *a*), as well as in their antenna to increase the rate of photon absorption. Chlorophyll *a* absorbs strongly in the blue-green and red regions of the light spectrum and the absorbed excitation energy is used to promote the photochemical reaction described by (B1) in Appendix B. The blue-green, or *Soret*, absorption band absorbs both downwelling and upwelling light within the water column and, hence, depletes the outbound radiation from aquatic environments of blue and blue-green photons. The magnitude of this absorption is used to quantitatively derive the concentration of photosynthetic pigments in the upper portion of the water column and is the basis for estimating phytoplankton concentrations from space.

To a first order approximation, the concentration of phytoplankton pigments can be quantitatively related to the photosynthetic rate (Fig. 2). The relationship between these two parameters is causal, albeit empirical, because, to a first-order approximation, the concentration of chlorophyll *a* is proportional to the number of photosynthetic reaction centers. In fact, if the quantum yield of photosynthesis was constant, photosynthetic rates would be directly proportional to the rates of irradiance and chlorophyll *a* concentrations. However, quantum yields are not constant and a wide range of productivity models have been developed to estimate phytoplankton photosynthesis

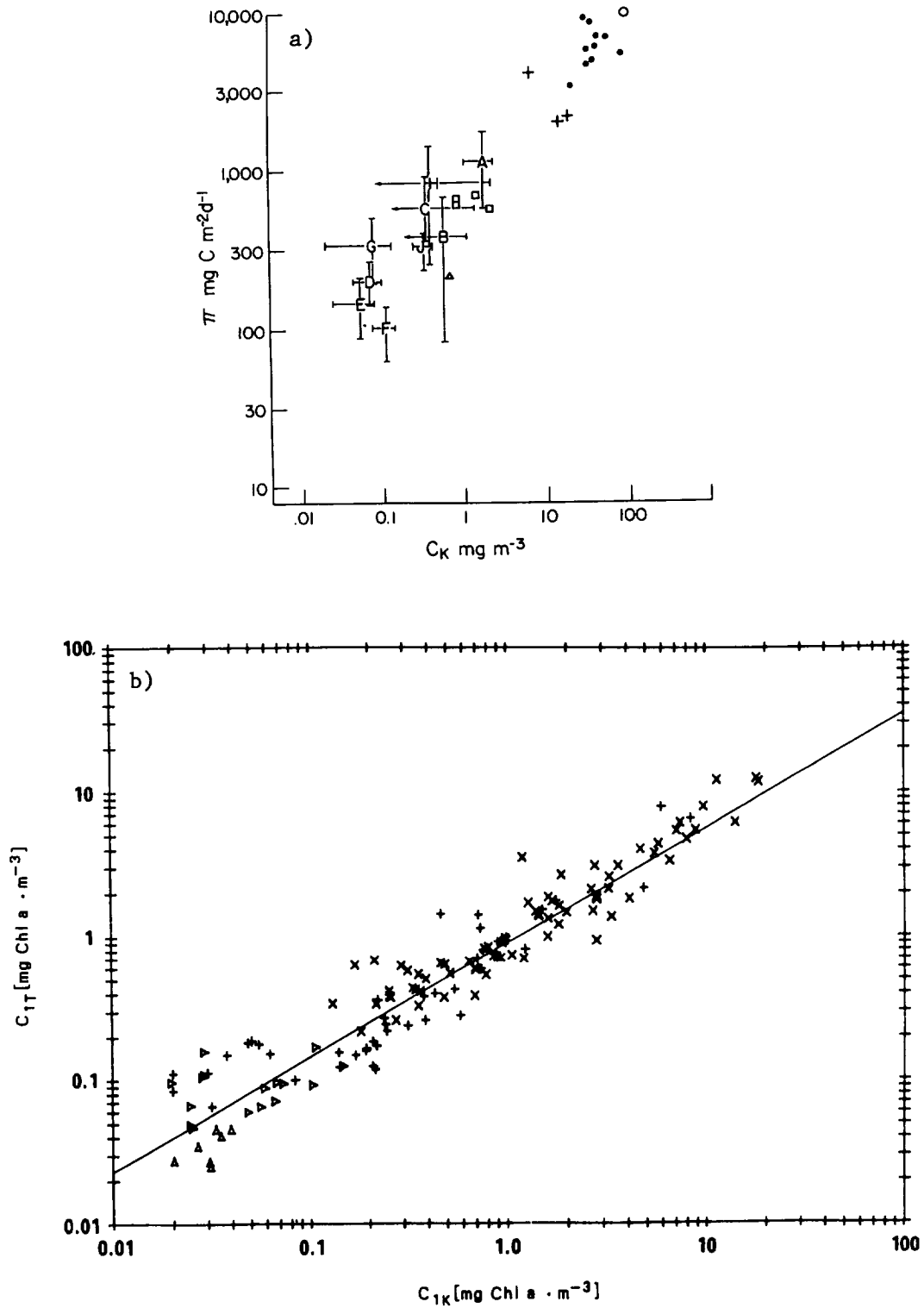


Fig. 2. Empirical relationships between surface chlorophyll concentration (C_K) and depth-integrated primary production (Π or P_T): a) from Eppley et al. (1985), reproduced by permission from Oxford University Press; and b) from Smith and Baker (1978), reproduced by permission from *Limnology and Oceanography*.

from satellite-derived chlorophyll fields; each differing with respect to assumptions made regarding the variability in quantum yields.

An algorithm that calculates annual primary production from annual composites of phytoplankton chlorophyll in the world ocean has been proposed for the MODIS morning crossing (AM-1) mission. This annual productivity algorithm will be applied to SeaWiFS data prior to the launch of MODIS and will compute annual productivity from annual mean surface chlorophyll fields and a single linear regression equation. This empirical equation applies to oceanic regions where episodic surface phytoplankton blooms occur, as identified by the mean and variance in surface chlorophyll measured by a satellite. The linear regression equation, however, does not apply to regions that often have a wide range of annual primary production, but do not exhibit surface phytoplankton blooms. These regions can be distinguished from the former based on their low mean and variance in satellite-derived chlorophyll. For regions where the regression equation applies, a running-average annual primary productivity will be computed at subannual temporal resolution (e.g., daily, weekly, or monthly). It is not yet clear how annual primary productivity will be computed within regions where the regression equation does not apply. What is clear, however, is that the assumption of a constant quantum yield for photosynthesis, on which the annual primary productivity algorithm is based, is an oversimplification for the world ocean.

Chlorophyll is a pool, while primary productivity is a flux. To derive a flux from a pool, a time-related variable must be incorporated. Time-dependent models of photosynthesis are developed by incorporating irradiance, where the transfer function is the quantum yield. A variety of such models have been described (Table 2) that differ, not so much in concept, but in the level of complexity regarding description of the state variables. Development of robust, time-dependent models of global photosynthetic processes is critical for at least three reasons.

1. Such models permit short-term, e.g., daily, calculations of photosynthetic rates. *In situ* measurements are based on short-term incubations; hence, compatibility in the time scales between measurements and models requires time-dependent models. Time-scale compatibility is requisite for evaluating algorithm performance.
2. Short-term measurements can provide a quantitative assessment of quantum yields. Modeling the changes in quantum yields is problematic at present, but essential for prognostic applications in integrated, global biogeochemical cycle models. Hence, short-term measurements and modeling efforts permit an understanding of the behavior of key variables that govern photosynthetic rates.
3. Among the strongest biogeochemical signals that integrate photosynthesis and respiration on a global scale

are the seasonal oscillations of CO_2 and O_2 in the atmosphere (Fig. 3). The CO_2 and O_2 signals reflect rates of carbon fixation on land and in the ocean, with O_2 cycles containing a proportionally larger contribution from the ocean. This is because the short-term exchanges of CO_2 between the atmosphere and the ocean are damped by the buffering of the carbon system in seawater. The amplitude of the CO_2 oscillation has been used to infer global net carbon fixation by *terrestrial* biota, while the combined cycles have been used to infer rates of carbon fixation by *marine* biota. Interhemispheric differences and interannual variations in CO_2 , O_2 , and the isotopes of CO_2 have been used to infer the hemispheric-scale spatial patterns and interannual variations in the contribution of the marine and terrestrial components of the carbon cycle. Subannual models of oceanic carbon fixation are essential for constraining the seasonal and interannual global carbon budget, and for determining changes in the biological pump.

The fundamental goal of the OPPWG is to iteratively develop, compare, test, and implement standardized algorithms that calculate oceanic photosynthesis from satellite observations of ocean color. This effort is an ongoing, long-term, multimission, international exercise which uses both numerical and observational systems. The initial goal is to develop and select a time-dependent primary productivity algorithm for operational use within two years after the launch of SeaWiFS and to iteratively improve that algorithm with the launch of MODIS and the Medium Resolution Imaging Spectrometer (MERIS) ocean color sensors. By using standard input variables such as chlorophyll *a*, the primary production algorithm selected will not be dependent on a specific sensor. This effort will provide the framework for quantifying ocean biological processes in the 21st century.

1.2.3 Time-Dependent Algorithms

Ideally, a time-dependent algorithm for routine calculations of ocean productivity will be based on a mechanistic model of the photosynthetic processes and primary production in the ocean. The consensus primary productivity algorithm will be selected according to the model's underlying construct and the requirement that satellite-derived surface chlorophyll fields are a primary forcing variable, although the algorithm might also use surface irradiance, sea surface temperature (SST), and satellite measured surface winds, along with ancillary historical data. An additional requirement for the selected algorithm is that the calculated product of the model is total primary production, not net photosynthesis (Appendix C).

Primary productivity algorithms are parameterized using *in situ* data sets containing both primary productivity measurements and ancillary model input variables (chlorophyll concentration, light, temperature, etc.). Productivity algorithms are often regionally prescribed to permit

Table 2. Classification system for daily primary productivity (ΣPP) models based on implicit levels of integration. Each category includes a photoadaptive variable [i.e., Φ , φ , $P^b(z)$, P_{opt}^b] corresponding to the resolution of the described light field. Φ and φ are chlorophyll-specific quantum yields for absorbed and available photosynthetically active radiation (PAR), respectively. Wavelength resolved models (WRMs) and wavelength integrated models (WIMs) are parameterized using measurements which approximate net photosynthesis and therefore, require subtraction of daily phytoplankton respiration (R) to calculate ΣPP . Time integrated models (TIMs) and depth integrated models (DIMs) are ideally, parameterized using measurements conducted over 24 h which approximate net primary production and thus, do not require subtraction of respiration. $P^b(z)$ and P_{opt}^b are chlorophyll-specific photosynthetic rates; the asterisk (*) indicates normalization-to-chlorophyll concentration (from Behrenfeld and Falkowski 1997a).

| Model Category | Generalized Model Structure |
|----------------|---|
| WRMs | $\Sigma PP = \int_{\lambda=400}^{700} \int_{\text{sunrise}}^{\text{sunset}} \int_{z=0}^{z_{eu}} \varphi(\lambda, t, z) \text{PAR}(\lambda, t, z) a^*(\lambda, z) \text{Chl}(z) d\lambda dt dz - R \uparrow$ |
| WIMs | $\Sigma PP = \int_{\text{sunrise}}^{\text{sunset}} \int_{z=0}^{z_{eu}} \Phi(t, z) \text{PAR}(t, z) \text{Chl}(z) dt dz - R \uparrow$ |
| TIMs | $\Sigma PP = \int_{z=0}^{z_{eu}} P^b(z) \text{PAR}(z) DL \text{Chl}(z) dz \S$ |
| DIMs | $\Sigma PP = P_{opt}^b \text{PAR}(0) DL \text{Chl } z_{eu}$ |

$\uparrow z_{eu}$ is depth of the euphotic zone.

$\uparrow t$ is time.

$\S DL$ is day length.

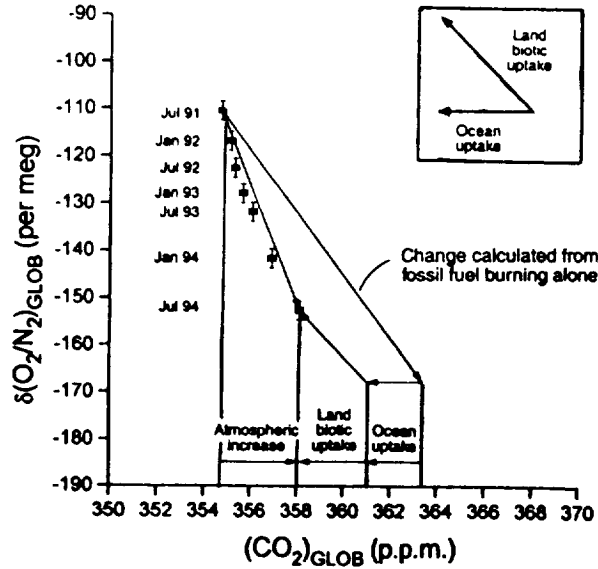


Fig. 3. Variations in the atmospheric O_2 abundance from air samples collected at stations in the Northern and Southern Hemispheres in relation to the global CO_2 [i.e., $(CO_2)_{GLOB}$] in parts per million. The variations are reported as changes in the global $O_2:N_2$ [i.e., $\delta(O_2:N_2)_{GLOB}$] calculated as $(O_2:N_2) = [(O_2/N_2)_{\text{samp}} / (O_2/N_2)_{\text{ref}} - 1] \times 10^6$. A decreasing trend in O_2 abundance is observed at all stations. This is driven largely by the consumption of O_2 by the burning of fossil fuel, but is also sensitive to exchanges with terrestrial biota and the ocean. Seasonal cycles in O_2 abundance are also observed at all stations. These cycles reflect seasonal exchanges of O_2 with terrestrial biota and the ocean. At the Northern Hemisphere stations, terrestrial biotic and oceanic exchanges contribute roughly equally to the cycles, while oceanic exchanges dominate in the Southern Hemisphere. The oceanic exchanges are a reflection of seasonal variations in the strength of the biological pump in the ocean. In both hemispheres, the maximum in the cycle occurs in late summer. Small interannual difference in the shape and magnitude of these cycles at Cape Grim can be noted. These variations possibly arise from year-to-year modulations in the strength of the marine biological pump. This figure is from Keeling et al. (1996). Reprinted with permission from *Nature*, Macmillan Magazines Ltd.

quantum yields to vary spatially and temporally. That is, different sets of parameters are assigned to various oceanic regions in a manner analogous to primary productivity maps developed for terrestrial ecosystems, an approach which necessitates a strategy for determining boundaries between regions, i.e., oceanic *provinces*). Preferably, such a strategy employs flexible boundaries determined by the forcing fields themselves, rather than using rigid geographic definitions based on climatologies. Regardless of the specific approach used to parameterize quantum yields, no current model accounts for all of the variance in this key parameter (Behrenfeld and Falkowski 1997a).

As briefly described, the relationship between photosynthesis and irradiance is the core of all time-dependent primary production models. Most primary productivity models can be shown to be mathematically equivalent when expressed in the same units and when the relationship between parameters is understood (Table 2). A set of round-robin tests conducted by the OPPWG, and using a standard uniform data set supplied to individual investigators, however, yielded markedly different calculated values for primary production between models. These differences in algorithm performance can be traced to three key issues:

- a) Differences in parameterization;
- b) Differences in the level of integration; and
- c) Differences in model forcing.

These issues are addressed separately, below, along with recommendations to NASA on the direction basic research should take for improving model reliability in satellite-based estimates of global phytoplankton productivity. A better understanding would, thereby, be obtained of the ocean's role in the biogeochemical cycles of the Earth.

1.3 PARAMETERIZATION ISSUES

Although the radiocarbon method for measuring photosynthesis in aquatic ecosystems has been available since the early 1950s and has been widely adopted, the standardization of techniques, assurance of data quality, and widespread availability of high-quality data have lagged far behind. In response to the standardization and quality assurance issues, JGOFS and other programs have commissioned panels to recommend a set of protocols for measuring primary productivity and other relevant variables (Table 3). There are four overriding concerns in developing a recommended set of protocols for at-sea measurements of primary production:

- 1) Identifying what is being measured;
- 2) Formulating detailed procedures for measuring the chosen variables;
- 3) Validating measurements against other indices of production and the ability to specify levels of precision; and
- 4) Developing a sampling strategy recommending appropriate space and time scales of measurements.

Satellites can provide information on geographic position, SST, solar irradiance at the surface ocean, and an estimate of the average chlorophyll concentration within the upper 10–20 m of the surface. Thus, productivity algorithms for satellite applications are normally based on relationships between chlorophyll and surface irradiance, modulated by temperature and perhaps nutrients. The factor relating chlorophyll to irradiance (and temperature) can, in the simplest case, be a chlorophyll-specific rate of primary productivity or a physiological parameter of phytoplankton photosynthesis, i.e., a quantum yield.

Quality assurance of productivity measurement data is a particularly critical issue. Much of the data obtained during JGOFS field programs are quality assured to the best level of effort possible. However, all measurements of primary production from the open ocean made prior to about 1980 were made using sampling devices containing minor concentrations of trace metals that were potentially toxic to phytoplankton. Hence, primary productivity data obtained from the open ocean from the 1950s to about 1980 are often viewed as being of questionable quality. The historical problem of trace metal contamination is far less acute in data obtained from coastal waters.

The two most important data sets for model and algorithm comparisons are climatological monthly mean global chlorophyll fields, and incident solar irradiance fields. These, and other data sets required for such comparisons, are described below. Other common data sets may also be required. Ideally, these data sets should reside in a common format, e.g., a $1^\circ \times 1^\circ$ global grid, easily accessible to all who wish to test their model and algorithm on regional-to-global scales. The preliminary list of data sets required for these comparisons includes 12, monthly-resolved:

- i) Satellite-based chlorophyll fields on a global $1^\circ \times 1^\circ$ grid;
- ii) Incident PAR fields interpolated to a global $1^\circ \times 1^\circ$ grid;
- iii) Incident SST fields interpolated to a global $1^\circ \times 1^\circ$ grid; and
- iv) Mixed-layer depths interpolated to a global $1^\circ \times 1^\circ$ grid.

At present, there is no standard data set used to parameterize primary production algorithms, nor is there a specific database used by NASA to facilitate algorithm development.

1.3.1 Recommendations

Systematic, long-term monitoring of selected aquatic and terrestrial habitats provides invaluable information in the effort of characterizing climate trends (Keeling and Shertz 1992) and the associated response of ecosystems (Woodwell et al. 1978). In this context, oceanic long-term time-series records of climate and biologically relevant variables are extremely rare, because of the costs and logistics involved. Repeated oceanic measurements are imperative

Table 3. Sources for measurement protocols applicable to productivity algorithms for satellite ocean color.

| Measurement | Reference |
|---|--|
| Primary Production | JGOFS (1991), Barber et al. (1996) |
| Photosynthesis vs. Irradiance Relationships | JGOFS Photosynthesis Measurements Task Team (1997) |
| Phytoplankton Absorption | Mueller and Austin (1995) |
| Ocean Optics | Mueller and Austin (1995) |
| Chlorophyll <i>a</i> | JGOFS (1991), Mueller and Austin (1995) |

for understanding natural processes that exhibit slow or irregular changes.

Recommendation: NASA should interact with other US and international agencies to support long-term measurement programs of ocean productivity.

Such an effort is essential for using primary productivity algorithms in prognostic models of climate change in biogeochemical feedbacks.

Global ocean color, SST, altimetry, and scatterometry time-series provide some of the relevant data required for monitoring environmental variables that affect aquatic photosynthesis. From these variables, and knowledge of the mechanisms regulating photosynthesis, semi-analytical models of water-column integrated net photosynthesis have been developed. To date, however, these models need specific parameterization for different regions of the ocean with different pelagic communities. Changes in ecosystem structure should be expected from long-term changes in environmental variables. For this reason, it cannot be assumed that model parameterization will remain constant if the ocean climate changes. Model parameterization over time, based on *in situ* time-series records, will be required to identify nonpredictable responses of the pelagic photoautotrophic community to long-term physical forcings.

Recommendation: The OPPWG recommends that NASA develop and maintain a central database, which would be accessible to all researchers, containing high quality and traceable primary production measurements from the world ocean and ancillary data to facilitate primary productivity algorithm development, testing, and standardization.

1.4 MODEL INTEGRATION LEVELS

A generic classification of primary production models (Table 2) illustrates that the fundamental difference in model structure is related to the level of integration.

Satellite measurements of ocean color can provide estimates of upper ocean pigment concentration. However, chlorophyll is not uniform throughout the water column in most regions of the world ocean and frequently subsurface chlorophyll maxima are observed near the bottom of the upper mixed layer. A considerable effort has gone into developing empirical algorithms that relate satellite-based

estimates of phytoplankton pigment concentration to the vertical chlorophyll structure. Often, this exercise has been concurrently accompanied by optical models that permit the explicit calculation of spectral irradiance at any depth at any time throughout the day. Hence, time-dependent, depth-resolved, spectral models [i.e., WRMs (Table 2)] were developed to calculate photosynthetic rates at each point in the water column throughout the day (Morel 1991, Bidigare et al. 1992, and Behrenfeld and Falkowski 1997b). These algorithms are often parameterized with local *in situ* measurements of photosynthesis in relation to irradiance and inherently emphasize the role of light absorption in controlling photosynthetic rates.

There are also productivity algorithms based on parameterizations of daily integrated primary productivity. These algorithms can be either depth-resolved or depth-integrated. Parameterization of these algorithms is based on measurements which inherently integrate variable photosynthetic rates over a day and often over depth. Both types of algorithms can be modeled in terms of two or three parameters: an initial light-limited productivity rate, a water column maximum value for productivity normalized to chlorophyll, and possibly a parameter characterizing photoinhibition at high light. The advantage of these semi-integrated algorithms is that their parameterization is more consistent with the level of integration associated with satellite data and *in situ* measurements. One could therefore argue that characterization of local-scale variations in photosynthesis-irradiance parameters is unnecessary, since satellite data are already integrated at the local scale.

In addition to models of primary production (listed in Appendix C), physiological models have also been developed which relate light absorption to growth, e.g., Sakshaug et al. 1989. These algal growth models are parameterized from laboratory studies of representative phytoplankton taxa and applied to global maps of satellite-derived chlorophyll. The rate of photosynthetic carbon fixation is calculated from the product of the carbon-specific growth rate and the phytoplankton carbon concentration. The advantage of this class of algorithms is that their parameters relate directly to the traditional parameterization of local-scale processes. Since photosynthesis is best understood at the cellular or molecular level, it is argued that

algorithms in this category will provide a better understanding of large-scale variations in primary productivity. A disadvantage of such algorithms is that the underlying physiological models are difficult to verify, since many of the key parameters are difficult to measure *in situ*, e.g., the carbon-to-chlorophyll ratios. Hence, there are no long-term, large databases for parameterization of algorithms based on *in situ* measurements.

Algorithms parameterized at the semi-integrated or local scale may not be appropriate at the scale of the satellite pixel, i.e., level-2 data, and even less appropriate at the larger scales of level-3 data. Scaling issues are particularly relevant if the primary productivity algorithm is nonlinear with respect to its independent variables and/or if there is covariance among the independent variables. Substituting the mean of input variables (e.g., mean chlorophyll, mean light, etc.) into a nonlinear function will not, in general, produce the mean of the dependent variable. The greater the variance within the domain, the greater the error. Ideally, algorithms used for satellite-based productivity estimates should yield unbiased estimates of mean primary productivity within the space-time domain of the level-2 or level-3 data.

1.4.1 Algorithm Evaluation and Selection

A central goal of the OPPWG is the evaluation and selection of a consensus time-dependent algorithm applicable to both local and global chlorophyll maps. When applied to level-2 data, the algorithm will yield an estimate of daily integral primary productivity (in units of $\text{gC m}^{-2} \text{d}^{-1}$) at every pixel for which phytoplankton chlorophyll is derived. Thus, its output can be compared, for example, with primary productivity time-series measurements made at discrete sites with quality assured *in situ* measurements, such as the Hawaii Ocean Time-Series (HOTS) and Bermuda Atlantic Time-Series (BATS) stations. When applied to level-3 data, the short-term algorithm should produce an estimate of the mean daily integral productivity within spatial resolution elements (i.e., bins) of approximately $9 \times 9 \text{ km}^2$, and averaged over time periods of 1 day, 8 days, 1 calendar month, and 1 year.

To reach the goal of selecting and implementing a consensus, time-dependent, primary productivity algorithm within two years after the launch of SeaWiFS, the following four-part strategy is recommended.

- 1] Continue the Primary Productivity Algorithm Round-Robin (PPARR) experiments.

The first primary productivity algorithm round-robin (PPARR-1) was completed in October 1995 and an informal report was circulated for comments. There were 11 participants and 15 algorithms were tested. The performance of the algorithms was regionally variable and, thus,

a composite algorithm based on differing regional parameterizations was suggested.

PPARR-2 was completed and the results are being prepared for publication in a peer-reviewed journal. PPARR-2 includes three times more stations than PPARR-1, with wider seasonal and geographic coverage. Data for each of the stations was distributed to participants in a series of three steps, with progressively more information given at each step. This stepwise procedure allowed scientists to determine what information is most useful for improving algorithm performance. This round was also designed to estimate the effect of errors in satellite chlorophyll.

The plans for PPARR-3 have been formulated. In PPARR-3, seasonally- and spatially-resolved calculations of global primary production produced by various algorithms based on a common set of forcing fields will be compared. Several groups have recently produced seasonally-resolved calculations of ocean primary production at approximately $1^\circ \times 1^\circ$ spatial resolution (Yoder et al. 1993, Longhurst et al. 1995, Antoine et al. 1996, and Behrenfeld and Falkowski 1997b). All of these calculations are based on global CZCS chlorophyll fields, but other forcing variables (e.g., incident solar irradiance, integration depth, and SST) differ among the groups. In fact, the specific version of the monthly mean CZCS chlorophyll fields also differs among groups. Nevertheless, preliminary analyses indicate that the space and time agreement between the different approaches appears to be quite good in that the global patterns are similar and change seasonally in comparable ways. However, model agreement needs to be quantified more explicitly; also, where and when calculated primary production differs and by how much (Table 4) needs to be determined. This is critical information for selecting the standard, short-term algorithm to be implemented by NASA and to understand how that algorithm relates to others. The comparison may also help indicate priority areas for *in situ* studies.

- 2] Establish the criteria for selecting the consensus algorithm.

Based on results of the first and second round-robin experiments, it is anticipated that there will be several algorithms that are equally valid in terms of their root mean squared (rms) errors. Likewise, it is expected that objections to certain algorithms based on computational complexity will be overcome as strategies for implementing algorithms are improved. Thus, further criteria for selecting one algorithm for implementation are needed. Arguments for explicit (local) parameterizations may be compelling, but these arguments may become invalid if the integrated or scaled-up models (appropriate to level-2 and level-3 data) require radical changes in model parameterizations. Ultimately, the deciding criterion may be the ease with which scaling issues can be reconciled with verifiable observations.

Table 4. Global annual phytoplankton primary production (in units of PgC y^{-1}) calculated with the vertically generalized production model (VGPM) from Behrenfeld and Falkowski 1997b), *Laboratoire de Physique et Chimie Marines* (LPCM) model (Antoine et al. 1996), Bedford Production model (BPM) (Longhurst et al. 1995), and the Eppley and Peterson (1979) compilation (E&P). Annual production is also shown for the five major ocean basins defined by Antoine et al. (1996) (percentages of total production indicated in parentheses), as well as three trophic categories for the VGPM and LPCM models (subpolar plus global in brackets) (from Behrenfeld and Falkowski 1997b).

| Integration Area | Category | VGPM | LPCM ^a | BPM ^b | E&P ^c |
|------------------|-----------------------|--------------------------|-------------------|---|------------------|
| Ocean Basin | Global Total | 43.5 | 46.9 | 50.2 ^{46.5} _{44.7} | 27.1 |
| | Pacific | 16.7 (38.3) | 20.0 (42.7) | 19.4 ^{18.1} _{17.4} (38.6) | 9.1 (33.7) |
| | Atlantic ^d | 11.9 (27.5) | 11.3 (24.0) | 13.7 ^{11.7} _{10.8} (27.3) | 8.6 (31.6) |
| | Indian | 6.2 (14.2) | 8.1 (17.3) | 6.5 ^{6.2} _{6.0} (13.0) | 6.0 (22.0) |
| | Arctic | 0.4 (0.9) | 0.6 (1.3) | 1.4 (2.8) | 0.1 (0.5) |
| | Antarctic | 8.3 (19.1) | 6.9 (14.7) | 9.2 (18.3) | 3.3 (12.2) |
| Trophic Category | Oligotrophic | 10.3 [10.5] ^e | 16.2 | | |
| | Mesotrophic | 22.0 [26.4] ^e | 22.5 | | |
| | Eutrophic | 3.6 [6.6] ^e | 2.5 | | |

- a. All LPCM production values are for model results when the contribution of phaeopigments to C_{sat} is negligible. LPCM production values were recalculated by Antoine using the identical CZCS pigment data used for the VGPM calculations and, thus, differ slightly from results reported by Antoine et al. (1996).
- b. Annual production values for the BPM using standard values for model variables are indicated by the larger numbers. The superscript and subscript values are annual production estimates when nonalgal particulates in turbid coastal waters reduce the active chlorophyll component of water-leaving radiance by 50% and 75%, respectively.
- c. Division of annual production into the primary ocean basins is taken directly from Eppley and Peterson (1979) and may not correspond exactly to divisions described by Antoine et al. (1996).
- d. Annual production for the Mediterranean Sea is included in the Atlantic Ocean production.
- e. The three trophic categories were defined using annual average C_{sat} as: oligotrophic = $C_{\text{sat}} \leq 0.1 \text{ mg m}^{-3}$; mesotrophic = $0.1 \text{ mg m}^{-3} < C_{\text{sat}} \leq 1 \text{ mg m}^{-3}$; and eutrophic = $C_{\text{sat}} > 1 \text{ mg m}^{-3}$ (Antoine et al. 1996). Trophic productivity was reported by Antoine et al. (1996) for latitudes between 50°N and 50°S. For comparison, trophic production values for the VGPM are shown for the same latitudinal band, but global values (90°N to 90°S) are included in brackets.

3 Compare the algorithm performance during the first two years after the SeaWiFS launch.

It is important for the entire scientific community to have the opportunity to use and be able to assess the existing models to estimate primary production from remotely sensed ocean color data. The community will be encouraged to use (and compare) the output of primary productivity models for a wide range of science applications, such as input to food-web or carbon-cycle models. Open availability of the various research products will be instrumental in selecting a standard, short-term algorithm and will contribute to understanding the viability and differences between algorithms used to estimate primary production from space. Two years of widespread use of the different model products and an ongoing series of round-robins will provide a test bed of the various modeling approaches and implementations.

The availability of primary production model output by the individual investigators on behalf of the research groups is to be understood as a courtesy. In this regard,

NASA and JGOFS will cooperate to extend the use of their data sets beyond their own scientific research groups. The data are research products and, as such, are subject to uncertainties and likely evolution and refinement. They are not sanctioned by NASA, nor are they guaranteed by the original research groups. If the data are used for research purposes leading to publication or public presentation, the original research group must be notified and acknowledged.

Recommendation: The OPPWG recommends that with the successful launch of SeaWiFS, the various research groups working on algorithms provide their monthly primary productivity estimates using SeaWiFS chlorophyll fields for the global ocean, with gridded data sets provided (not simply images).

These data should be made available on the World Wide Web via anonymous file transfer protocol (FTP). Furthermore, the OPPWG proposes that NASA create an Ocean Primary Productivity Homepage to provide links to these research products.

4 Determine error fields for the selected algorithm.

Error fields associated with an algorithm will be scale dependent. Thus, there will be different error fields for the various level-2 and level-3 products. With the round-robin experiments, attempts are being made to determine the errors associated with point estimates. In other words, how well does the algorithm estimate integral productivity at a particular location? It should also be determined as to how well the algorithm estimates the mean productivity over a spatial and temporal domain. If the algorithm errors are unbiased, then they should decrease with increases in the size of the domain. It will be difficult to quantify this error based on surface measurements because ship sampling is highly restricted in coverage. Thus, for example, there are no true monthly average productivity measurements at regional scales to compare with satellite level-3 products.

Research questions related to determining error fields between algorithms include:

- a. What is the impact of space-time variances on error propagation for chlorophyll and primary productivity algorithms?

This question relates directly to the scaling issues discussed above. There may be a need for specific field experiments to address questions of the short-term spatial and temporal variance and covariances among algorithm parameters.

- b. What is the sensitivity of daily integral primary productivity to the input variables in the models or algorithms?

How much better can the integral productivity be estimated at a particular location with a better, more precise knowledge of surface chlorophyll, surface irradiance, or surface temperature? How much better are regional estimates of productivity given the same input and the coverage afforded by satellite data?

- c. When all algorithms are parameterized with data from a specific region, how do they compare?

Are regional differences in algorithm performance the result of different parameterizations, or are the underlying processes being modeled differently?

- d. How will the boundaries between regions be determined?

The method to be chosen should allow for variations in the boundaries driven by natural or anthropogenic forcings.

- e. How should the annual, global-scale algorithm compute primary productivity in regions where productivity does not result in seasonal phytoplankton blooms?

In such regions, the model forcing is extremely critical (Sect. 1.5).

Recommendation: The OPPWG recommends that primary productivity and photosynthesis-irradiance measurements be made in conjunction with optical and other biological measurements on the scheduled calibration and validation cruises for SeaWiFS, MODIS, and activities supported by SIMBIOS. It is also recommended that the SeaWiFS Project implement a "primary productivity index."

This index might have the same units as primary productivity, but not necessarily claim to be an accurate estimate of productivity compared with radiocarbon measurements. The value of the index is that it will afford a view of interannual differences throughout the lifetime of SeaWiFS and follow-on sensors.

1.5 MODEL FORCING

Provided that satellite measurements of phytoplankton chlorophyll biomass are available, the key remaining scientific issue for all productivity models is: What causes variations in quantum yields in the world ocean? Satellite estimates of primary production can be developed for a variety of time and space scales to address this problem.

1.5.1 Temperature

On a global spatial scale, one of the major determinants of primary productivity is temperature. Temperature can directly affect quantum yields by limiting the rate at which carbon dioxide is fixed through enzymatic reactions; satellites can provide reasonably good estimates of SST. There is virtually no consensus, however, on how to parameterize the effects of temperature on primary productivity (Fig. 4). This lack of consensus is a consequence of the varied secondary effects of temperature on photosynthetic energy conversion efficiency [e.g., changes in temperature (ΔT) are correlated to changes in nutrient availability (see below)] and physiological acclimations to temperature which induce a great deal of variability in temperature-photosynthesis relationships. It is clear, however, that the primary influence of temperature is on the maximum rate of photosynthesis at light saturation. This rate is not directly dependent on light absorption, yet critically determines the water column quantum efficiency (Behrenfeld and Falkowski 1997a and 1997b).

Historical data demonstrate that in many regions of the world ocean, nutrient concentrations (nitrate, phosphate, and silicate) can be estimated from climatological databases of temperature. Such temperature-nutrient relationships appear to change regularly with latitude and longitude and can be used to provide unique temperatures (i.e., an index) at which nitrate, phosphate, or silicate become unmeasurable. At temperatures below this index, nutrient concentrations can be estimated using climatological correlations (Kamykowski and Zentara 1986), while

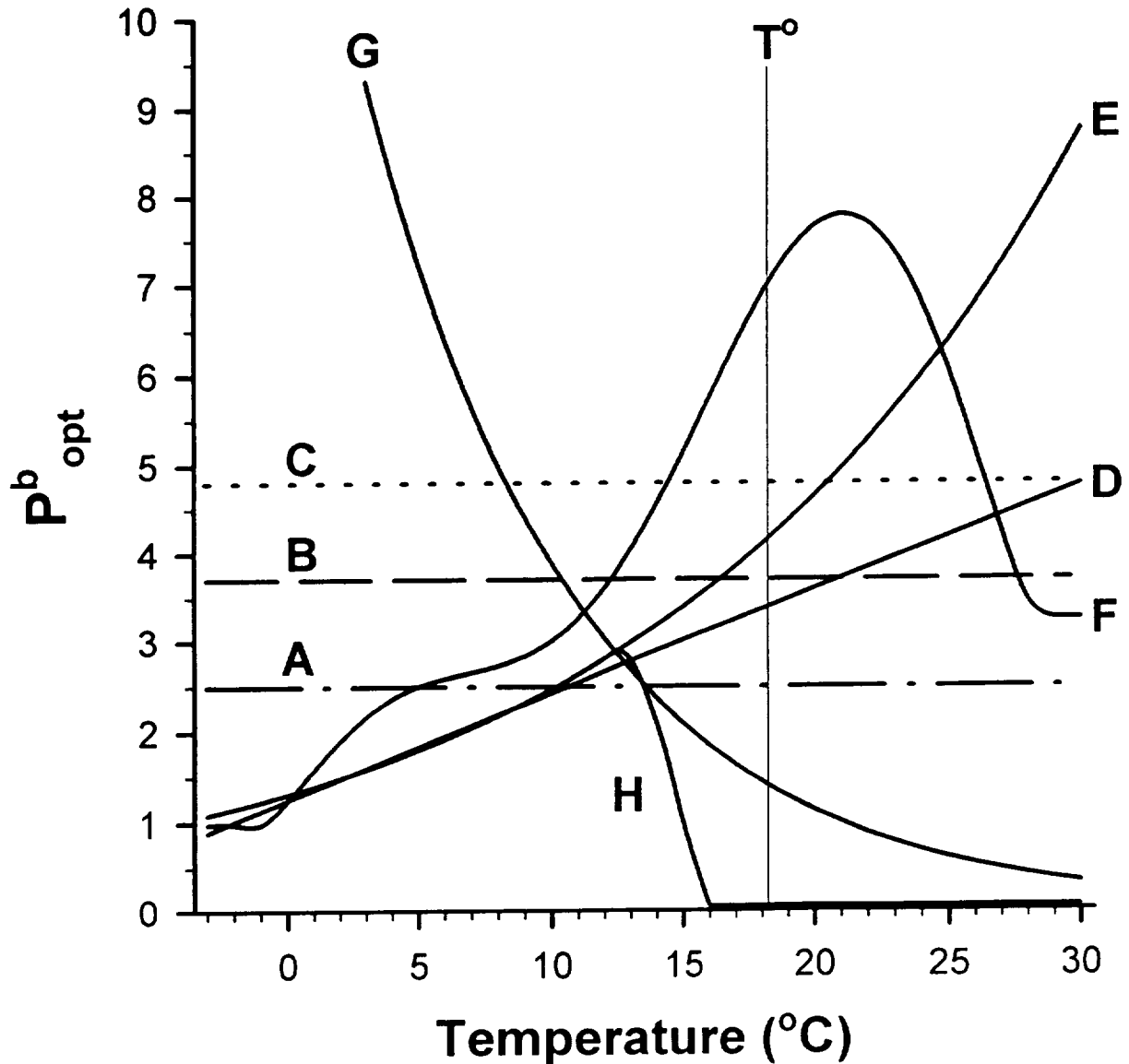


Fig. 4. Various models used for estimating the maximum chlorophyll-specific carbon fixation rate within a water column (P^b_{opt}). The curves A–H are defined as: A is the calculated value implicit in the Ψ model of Falkowski (1981); B is the Ryther and Yentsch (1957) estimate of $3.7 \text{ mgC (mgChl)}^{-1} \text{ h}^{-1}$; C is the Cullen (1990) revised value of $4.8 \text{ mgC (mgChl)}^{-1} \text{ h}^{-1}$ for B; D is the Megard (1972) model converted to hourly rates by dividing by 13.7 hrs.; E is the Eppley (1972) equation for the maximum specific growth rates converted to carbon fixation by normalizing to $4.6 \text{ mgC (mgChl)}^{-1} \text{ h}^{-1}$ at 20°C following Antoine et al. (1996); F is the Behrenfeld and Falkowski (1997b) seventh-order polynomial model; G is from Balch et al. (1992); and H is from Balch and Byrne (1994). T° is the Levitus climatological median upper ocean temperature (18.1°C) as computed by Antoine et al. (1996). (This figure is from Behrenfeld and Falkowski 1997a.)

above this index nutrients appear to be depleted. Satellite-based estimates of SST can provide a measure of nutrient concentration at the surface if temperatures are below the index or, alternatively, a measure of the ΔT that must be overcome by mixing if the SST exceeds the index. The ΔT estimates may be used with other estimates of mixed layer depth and vertical mixing to estimate nutrient flux to the near-surface region.

The different temperature indices at a geographic location also can be used to estimate which nutrient (e.g., nitrate or silicate) becomes depleted first. For example, in the Southern Hemisphere, the temperature at which silicate is unmeasurable tends to be colder than the temperature where nitrate becomes unmeasurable. In the Northern Hemisphere, nitrate tends to be below detection at a colder temperature than silicate. Therefore, SST may produce information that relates to the growth limitation of diatoms (silicate limitation) relative to nonsilicate-requiring phytoplankton. This information may be useful both in constraining quantum yields at a given geographic location and in relating total primary production to new production.

1.5.2 Time Dependency

At the annual and global scale, steady-state assumptions applied to quantum yield are perhaps logical; however, at shorter time scales or smaller space scales, time-dependence of quantum yields becomes necessary. This time dependence can be incorporated into a consideration of quantum yields in various ways. On daily scales, the diurnal variation in light intensity provides one source of variable forcing. This approach, however, ignores changes in vertical and horizontal physical processes that can influence how phytoplankton cells move around in the vertical water column. These cells typically have quantum yields that are not optimal for the environmental conditions which exist in the water column. This lack of equilibrium can constitute variability to primary production estimates that can be approached with present satellite capabilities by colocating different satellite measurements in space which were proximately collected. Existing physical models facilitate this data coordination. Future multisensor satellites will produce information on several biological and physical ocean characteristics that are collected at the same place and at the same time. The main point is that the estimates of primary production can be improved if information on water column physics, in terms of dynamic mixed layers and advection into pixels, is eventually included when considering quantum yields.

1.5.3 Research Issues

The critical importance of improving the characterization of physiological forcing factors in primary productivity models is becoming increasingly clear. There are two research questions of particular importance.

1. What controls the light-saturated rates of photosynthesis in phytoplankton and how can these rates be better represented in primary production algorithms?

It is basically understood that light saturated photosynthetic rates, normalized to chlorophyll biomass, are correlated with the ratio of the carboxylating enzyme, ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) to the number of photosynthetic reaction centers. However, Rubisco activity and structure are highly variable, unlike photochemical reactions where the basic molecular structure is highly conserved in all oxygenic photoautotrophs. There are few studies of Rubisco in relation to key physical forcing processes in phytoplankton. This situation is in sharp contrast to terrestrial primary production efforts, where studies of Rubisco activity have played a key role in formulating models of photosynthesis.

Recommendation: The OPPWG recommends that NASA develop collaborative research programs with the National Science Foundation (NSF), the US Department of Energy (DOE), and perhaps the US Department of Agriculture (USDA) to better understand the factors regulating Rubisco and the maximum photosynthetic rate in phytoplankton.

Such an effort is critical to developing prognostic models of the ocean carbon cycle.

2. What are the scales of variability in quantum yields and how are they related to physical circulation and turbulence?

Measurements of quantum yields of photochemistry can be made rapidly and in real time using variable fluorescence techniques. Results from such studies reveal both meso- and basin-scale variability in photosynthetic energy conversion efficiency. To a first order approximation, the variability appears to reflect nutrient limitations that constrain the ability of phytoplankton to synthesize critical components in the photosynthetic apparatus. Experimental manipulations, such as the addition of nutrients, often restore high quantum yields within a day.

The fundamental issues related to variability in quantum yields and biogeochemical cycles concern the homeostatic adjustments. If ocean turbulence or nutrient additions from sources external to the ocean were to alter nutrient supplies, would quantum yields remain constant or change? Insofar as export production is higher when productivity is higher, and productivity is higher when nutrient fluxes are higher, one might consider that quantum yields can be related to export production. This proposition is testable on ecological time scales and, if supported, the inverse construct—when export production was high, the quantum yield of photosynthesis was high—could be inferred. This latter issue provides a potential access for relating estimates of export production in the sedimentary record to the quantum yield of photosynthesis (hence,

nutrient fluxes) on geological time scales. It also permits prognostic calculations on ocean carbon fixation from ocean circulation models and other surrogate measures of nutrient flux (Appendix D).

1.5.4 Implementation

The overall approach for implementing Ocean Primary Productivity products was described in the MODIS Primary Productivity Algorithm Theoretical Basis Document (ATBD No. 25). It outlines a two-phase, quasi-parallel approach. Research leading to selection of a short time period algorithm will be conducted by the SeaWiFS Project and international investigators, with the OPPWG serving as a coordinating body. The Working Group was organized as a joint activity between the SeaWiFS Science Team investigations and the MODIS Instrument Team investigations. This group's goal was to have a selected algorithm within two years following the successful launch of OrbView-2 (formerly known as SeaStar), the SeaWiFS spacecraft, since validation and other consistency checks were deemed crucial for making any decision among the several theoretical approaches available at the time. The SeaWiFS Project would then implement the selected product in conjunction with planned annual reprocessing of SeaWiFS data.

The second path for implementation within EOS is via the MODIS Instrument Team and the EOS PGS. The development of an annual empirical algorithm was selected in the Execution Phase process; the development of this algorithm has maintained delivery schedules for software required by EOSDIS in order to meet the AM-1 launch readiness. The implementation of a short-term algorithm was deferred to research product status consistent with the OPPWG process. As initially envisioned, given the SeaWiFS launch schedule, comparisons of candidate algorithms within the OPPWG would be accomplished in sufficient time to incorporate the selected short-term algorithm for MODIS as an immediate postlaunch product. This would ensure that the data products would be consistent and the long time series would begin with SeaWiFS data.

For MODIS, this approach was dependent on the launch of OrbView-2 and experience with real data, as well as the planned approach for EOSDIS and its capacity to support research products and to absorb postlaunch implementation loads. Neither of these requirements has stood the test of time. Because of budget austerity, EOSDIS has no capacity for routine research products for the AM-1 mission, and little capacity to implement new postlaunch standard products except as required for the afternoon crossing (PM-1) mission. Research product development and generation is viewed by EOSDIS as within the purview of the Science Computing Facilities (SCFs), but these are insufficiently supported or scoped to provide routine generation and distribution.

In June 1996, the OPPWG reaffirmed its goal of selecting a consensus, short-term algorithm two years following the SeaWiFS launch. A reasonable schedule makes this selection probable in February 1999. In relation to EOSDIS code delivery schedules, these dates are not inconsistent with implementing a short-term algorithm for the MODIS PM-1 launch in December 2000, as well as a postlaunch product for MODIS AM-1 at that time.

Recommendation: In the June 1996 meeting, the OPPWG also recommended that NASA begin developing a simple primary productivity index for short time periods, to be implemented soon after the MODIS launch, as a research product available to the community to aid in evaluating analytical algorithms.

The group was unable to make a recommendation among several choices for the same reasons that selection of a consensus global algorithm is dependent on developing protocols, comparison criteria, and experience with real data.

1.5.4.1 Relation to SIMBIOS

Since several sensors are expected to produce global chlorophyll data fields, which are the key input product for both short- and long-term primary productivity models, the findings and products of the SIMBIOS effort bear heavily on this issue. The goals of SIMBIOS are to perform product comparisons, develop appropriate scientific merging procedures, and produce combined data products from multiple sensors to permit higher frequency global coverage than would be possible from a single sensor. This will begin with the SeaWiFS data sets. The timetable for the availability of such products is still to be determined, but to a first order approximation, this should not be too far removed from the selection of a consensus algorithm by the OPPWG. Also, suitability of chlorophyll fields for use in primary productivity estimation is a primary goal of the effort. As presently structured, however, production of a primary productivity product is beyond the scope of SIMBIOS.

1.5.5 Implementation Recommendations

The MODIS Standard Product algorithm development effort will proceed with the following modifications. Since the linear annual total production algorithm applies only in high-variance regions, a nonlinear approach will be incorporated for low-variance regions. To minimize increases in required computing capacity and storage, a simple global index could be computed on weekly, 9.5 km scales. These could be added as a field to the planned 8-day (weekly) product. The code to do so will be EOS compliant and will meet all the requirements of the EOSDIS Core System (ECS). Moreover, the code could be implemented with SeaWiFS data, since suitable *translators* from SeaWiFS level-3 to MODIS level-3 data formats are virtually complete. These translators were developed to enable SeaWiFS data to be used as seed data products for the MODIS

annual algorithm, such that the first 8-day MODIS level-3 chlorophyll data is combined with 44 such 8-day products from SeaWiFS to form the first running annual average. In this way, the ATBD No. 25 product generation begins at launch rather than launch plus 1 year.

The ATBD No. 25 SCF was being scoped to produce the SeaWiFS annual weekly running averages required as precursors to MODIS. The approach described above for generating and distributing the research product requires more computing capability and a distribution-access approach, which must be defined. Doing so solely within the SCF will require additional space and manpower, which are currently not included in GSFC planning. The choices are to:

- 1) Do this within the SCF;
- 2) Do this within the MODIS Team Leader Computing Facility (TLCF), which is roughly equivalent in function to the SeaWiFS calibration and validation element;
- 3) Do this jointly with the SeaWiFS Project, which could involve distributing the product from the SeaWiFS Project; or
- 4) Possibly send such products to the Distributed Active Archive Center (DAAC), although this is typically reserved for standard SeaWiFS products.

Discussions with the TLCF and the SeaWiFS Project need to begin immediately.

One suggested approach is that initially, the MODIS group perform the coding, handle the ancillary fields, and run the algorithm code with SeaWiFS level-3 products converted to MODIS format as input. Data would be made available through the Productivity SCF. Once the SeaWiFS processing system becomes routine, the SeaWiFS Project would assume routine operations as a new, post-launch, SeaWiFS data product. This is expected one year from the launch of OrbView-2. Data would then be available through the DAAC along with other SeaWiFS products. The MODIS PGS would implement the nonlinear algorithm at launch, using MODIS data, and the MODIS productivity algorithm would be available through the DAAC as a MODIS product. This dual stream of processing (SeaWiFS and MODIS) would continue until, and unless, appropriate methods for combining chlorophyll input is developed by SIMBIOS.

Upon selection of a consensus algorithm, the SeaWiFS Project and the MODIS PGS would convert to the new product as soon as acceptable code could be produced and tested. This product would replace the nonlinear algorithm, unless the OPPWG believe that the output data are nonredundant and important.

1.5.5.2 Product Delivered

The nonlinear primary productivity product would be produced on a weekly basis, at 9.5 km spatial resolution.

Alternatively, a daily product could be produced at the same spatial resolution from level-3 chlorophyll. A third alternative is to perform the calculation at the resolution of level-2 data and bin the data at daily, weekly, and annual periods. The volumes of data increase by roughly one and two orders of magnitude for the second and third alternative, respectively. The third approach would necessitate a significantly different processing approach.

1.5.5.3 International Collaborations

If a primary productivity algorithm is applied to satellite based maps of ocean chlorophyll rather than water-leaving radiances, it is, in principle, independent of the sensor and platform. Hence, the same algorithm could be applied not only to SeaWiFS and MODIS, but also to MERIS, or any other ocean color system that is used to derive chlorophyll. For this reason, primary productivity algorithms are inherently transparent to satellite databases of ocean color and are transportable from mission to mission. Given these properties, the development of ocean primary productivity algorithms benefits the international remote sensing community. The science plan developed here is supported by the international oceanographic research community through JGOFS and, by extension, the International Geosphere-Biosphere Programme (IGBP).

1.6 OCEAN BIOLOGICAL PUMP

Biogeochemical cycles are coupled. In the ocean, carbon fixation is itself limited by the availability of other essential plant nutrients, such as iron, fixed inorganic nitrogen, and phosphate. The historical geochemical construct of phosphate limitation in the global ocean is based on the hypothesis that nitrogen fixation will occur if nitrogen is limiting. This hypothesis was formed on an understanding of nutrient dynamics in lacustrine ecosystems and applied to the ocean. The hypothesis, however, is almost certainly incorrect for the ocean. It cannot be supported by the bulk distribution of either dissolved inorganic nitrogen (DIN) or dissolved inorganic phosphate (DIP) relative to the sinking flux in the contemporary ocean, nor is it consistent with either sedimentary records of enhanced biological organic fluxes or reduced denitrification rates during glacial maxima.

Phosphate sets an upper bound to carbon fixation. This bound is neither geochemically nor ecologically relevant as long as the sinking flux of N:P in organic matter exceeds that of the upwelling flux of inorganic nutrients, regardless of the relative turnover times of the two elements. The dissolved ratio of inorganic N:P in the ocean interior is approximately 14.7 by atoms. The corresponding elemental ratio in the sinking flux of organic matter is approximately 16.0. The difference in these two ratios, recognized by Redfield in 1958, is a consequence of a loss of inorganic nitrogen by the ocean through the process of denitrification. Nitrogen is resupplied via biological fixation. Hence, the ratio

of nitrogen fixation to denitrification critically determines the efficiency of the biological pump in the world ocean (Falkowski 1997).

Analyses of ice core records suggest that atmospheric CO_2 declined from approximately $270 \mu\text{mol mole}^{-1}$ to $190 \mu\text{mol mole}^{-1}$ over a period of about 5,000 years between the last interglacial-glacial maximum. Given a C:N of approximately 6.5 by moles for the synthesis of new organic matter in the euphotic zone, a simple box model calculation suggests that 240 Pg of inorganic carbon would have to have been fixed by marine photoautotrophs to account for the inferred change in atmospheric CO_2 . Such a change would have required an addition of approximately 7 Tg of fixed inorganic nitrogen per annum, resulting from an increase in biological nitrogen fixation. The inorganic pool size of NO_3^- in the world ocean is about 6,000 Pg. Hence, the change in the N_2 flux could have been as small as 0.0001% per year. Moreover, no net change in upper ocean alkalinity would be observed if N_2 fixation were accelerated during glacial periods, as the new nitrogen supplied to the ocean would be reduced to the equivalent of ammonium. The sink would have exerted a positive feedback, such that the initial forcing would have led to increased cooling if atmospheric CO_2 were removed by an enhancement of the biological pump.

The present, nonsteady state flux of CO_2 in the atmosphere ultimately will lead to a major redistribution of carbon in the major reservoirs. Insofar as the balance

between nitrogen fixation and denitrification will be either inadvertently altered by increased eutrophication on continental shelves or deliberately changed, the past and future role of the biological pump in affecting atmospheric CO_2 is large and cannot be ignored.

Over the next several decades, changes in atmospheric aerosol fluxes, radiation budgets, and ocean circulation will interactively affect ocean primary productivity and, potentially, the efficiency of the biological pump. Present models of global biogeochemical cycles are incapable of predicting the sign, let alone the magnitude, of this change in biological productivity over the world ocean. The major scientific tools for measuring and understanding such changes are observational systems, particularly satellite ocean color sensors. To that end, NASA will play an increasingly important role in helping to test key hypotheses related to the potential of the biological pump to influence atmospheric CO_2 levels.

1.7 CONCLUSION

The science plan presented here provides a framework within which to quantify the biological pump on daily, seasonal, annual, and decadal time scales. It is only through the implementation of such a plan that scientists can evaluate how, and to what extent, the ocean interacts with anthropogenic activities to affect biogeochemical cycles on Earth.

Chapter 2

Toward a Consensus Productivity Algorithm for SeaWiFS

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ABSTRACT

An OPPWG was formed to discuss the benefits and fundamental problems associated with using SeaWiFS and other ocean color satellite measurements for estimating oceanic primary production. During the first, and subsequent, OPPWG meetings, discussions focused on: 1) algorithm classification, including similarities and differences between currently available productivity algorithms; 2) algorithm parameterization and data availability; 3) algorithm testing and validation; and 4) the concept and benefits of a consensus SeaWiFS productivity algorithm. The productivity algorithms discussed range from simple statistical (empirical) relationships between surface chlorophyll concentration and photosynthesis, to complex theoretical models which derive time- and depth-specific photosynthetic rates from spectral models of irradiance distributions and depth-dependent chlorophyll distributions. Each classification of productivity algorithms has benefits and drawbacks. This report describes the results from the first OPPWG meeting and the scientific issues involved with developing a consensus SeaWiFS productivity algorithm.

2.1 INTRODUCTION

Photosynthetic fixation of inorganic carbon into organic material in the world ocean is driven almost entirely by phytoplankton, but the actual amount of carbon fixed is uncertain. While there is overwhelming evidence that phytoplankton carbon fixation plays an important role in maintaining the steady-state level of atmospheric CO₂, this process can affect the anthropogenic CO₂ concentration only if it is changing. Present state-of-the-art (not necessarily accurate) coupled ocean-atmosphere climate models predict changes in the thermohaline circulation of the ocean within the next century, and some observations suggest that thermal changes have already occurred (Roemmich and Wunch 1985). It is hypothesized

that these changes will stimulate phytoplankton biomass production in the nutrient-depleted areas of the open ocean. However, the effect on atmospheric CO₂ is uncertain, because the stoichiometric relationship between enhanced primary production and the air-sea exchange of atmospheric CO₂ is poorly understood. Thus, a major challenge for biological oceanographers is to determine whether oceanic primary production is in a steady state on time scales comparable with those for changes in atmospheric forcing. To achieve this goal, credible models must be made available which can accurately compute present and future productivity when ocean circulation patterns have changed.

In spite of the ability to remotely sense near-surface chlorophyll, the ability to predict total primary produc-

tion, given knowledge of near-surface chlorophyll, has remained elusive (Eppley et al. 1985, Platt and Sathyendranath 1988, Morel and Berthon 1989, Balch et al. 1992, and Balch and Byrne 1994). One problem in developing production models has been that the touchstone of sea truth has changed with time, because of such problems as trace metal contamination (Martin 1992) or simply differences in measurement techniques. A second problem is an inconsistency in model development and structure. Widely different models or algorithms have been developed, often based on different premises and data sets, making it virtually impossible to judge objectively which is the best based on how a model fits a given set of data (e.g., Balch et al. 1992). Finally, there has been an inconsistency in the data sets used to analyze various models. Thus, different models give different results with the same data sets (e.g., Balch et al. 1992), and different data sets give different results with the same models (e.g., Falkowski 1981, Platt 1986, Campbell and O'Reilly 1988, and Prasad et al. 1992).

With the launch of SeaWiFS, scientific expectations are high that some consensus emerges towards developing and improving global ocean primary production models. As a first step toward this goal, an OPPWG was formed with specialists in phytoplankton ecology, physiology, and productivity modeling. The first OPPWG meeting was held on 23–25 January 1994 and focused on:

- Clarifying what the characteristics of a *consensus* algorithm should be;
- What differences exist between currently available productivity algorithms;
- How algorithm testing procedures should be executed; and
- What are the benefits of developing a consensus algorithm in relation to the short-term goals of the SeaWiFS Project and the long-term goals of the scientific community.

This report discusses the outcome of that meeting and the advances made toward developing a consensus algorithm. This report is subdivided into three primary scientific issues:

1. Algorithm Classification
 - a. What type of information should the consensus algorithm provide?
 - b. What different types of algorithms are currently used and what are their characteristics?
2. Algorithm Parameterization
 - a. What input is required by productivity algorithms and how is this requirement met?
 - b. Can a consensus be reached on what sea truth is and, if so, what characteristics can be used to differentiate acceptable from unacceptable data?
3. Algorithm Testing and Validation
 - a. How can algorithm performance be tested objectively?
 - b. At what level should the consensus productivity algorithm be available to investigators using SeaWiFS data, and what information should be archived?

2.2 DISCUSSION RESULTS

2.2.1 Algorithm Classification

What type of information should the consensus algorithm provide?

Maps of primary production based on SeaWiFS ocean color imagery will be level-3 products obtained by averaging global area coverage (GAC) data to yield a horizontal resolution of about 9 km. In order to be compatible with imagery from other sources, such as the Advanced Very High Resolution Radiometer (AVHRR) and the Land Resources Satellite (LANDSAT), NASA will produce averages for time periods of 1 day, 8 days, 1 month, and 1 year. In particular, the SeaWiFS productivity algorithm should provide the oceanographic community with maps of annual global new and total production. The algorithm should also provide maps of 8-day averaged mean water column productivity. Finally, a mechanism should be available to provide, upon request of individual investigators, vertically resolved daily rates of photosynthesis. This high resolution product is very desirable since it will allow oceanographers conducting measurements of photosynthesis in the field to compare their rates with those modeled from SeaWiFS imagery.

What different types of algorithms are currently used and what are their characteristics?

Algorithms used to calculate total primary production from satellite remote sensing data range from simple empirical relationships to complex analytical models. Empirical models make broad generalizations about the relationship between satellite-based estimates of upper ocean chlorophyll and integrated primary production. These generalizations may be represented by a single regression equation which holds over several orders of magnitude (e.g., Eppley et al. 1985), or they may include additional terms, such as surface irradiance, light attenuation, and a photoadaptive term (e.g., P_{\max} , which is the light-saturated rate of photosynthetic carbon fixation), in an attempt to capture the fundamental factors driving integrated primary production. Empirical models generally require additional parameterization, or tuning, when extended to regions, or even seasons within a region, beyond those from which they were derived (e.g., Platt and Sathyendranath 1988, and Morel 1991).

Analytical models attempt to calculate photosynthesis using *first principles* of phytoplankton photophysiology

and light penetration through the water column, an approach which adds both physical rigor and increasing complexity. In a sense, analytical and empirical approaches are not as disparate as may first appear, since many of the photoadaptive coefficients used in analytical models, such as the initial slope (α) or the maximum rate (P_{\max}), are simply empirically-derived coefficients based on shipboard measurements. In addition, all productivity models rely on empirical relationships between the plankton population seen by a satellite and the photosynthetic populations in the deeper regions of the water column invisible to the satellite.

2.2.1.1 "Empirical" Models

The simplest empirical equations use only chlorophyll *a* to predict phytoplankton productivity integrated over daily, seasonal, or annual time scales (Smith et al. 1982, Eppley et al. 1985, and Campbell and O'Reilly 1988). Eppley et al. (1985) used standard ^{14}C -based estimates of daily productivity (d_{PC} , in units of $\text{mgC m}^{-2} \text{d}^{-1}$), along with average chlorophyll *a* concentrations (C_K , in units of mgChl m^{-3}), collected from a range of marine environments during various seasons, to calculate, using linear regression analysis, the empirical relationship:

$$\log_{10}(d_{PC}) = 3.0 + 0.5 \log_{10}(C_K), \quad (1)$$

which was revised using the data of Berger (1989) to:

$$\log_{10}(d_{PC}) = 2.793 + 0.559 \log_{10}(C_K). \quad (2)$$

A wide range of marine environments were represented in the data sets compiled by Berger (1989) and Eppley et al. (1985). Simply expanding the number of represented environments would likely not reduce variability in parameterization values of these seasonal productivity algorithms. Two approaches have been taken to expand the seasonal and spatial range of a given productivity algorithm:

- 1) Increase the integration time for primary production (decreased complexity); and
- 2) Increase the number of algorithm parameters (increased complexity) to reflect the primary factors resulting in the observed variability.

An example of the first approach is the development of a chlorophyll-based empirical algorithm for annual primary production. This annual primary production algorithm was parameterized using annual mean chlorophyll *a* concentration within the top optical depth (C_K , in units of mgChl m^{-3}) and measurements of daily phytoplankton particulate organic carbon production averaged monthly, then annually (P_{PC} in units of $\text{gC m}^{-2} \text{yr}^{-1}$). P_{PC} was calculated using the trapezoidal rule, while C_K was integrated using arithmetic averages of daily chlorophyll *a* for

each environment. In this manner, the annual primary production algorithm was calculated using linear regression analysis methods and data from oceanic and continental shelf regions of the Atlantic and Pacific Oceans as:

$$P_{PC} = 135.3 + 47.8 C_K. \quad (3)$$

Comparing measured and modeled P_{PC} indicates a strong regional-dependence of (3) performance.

The second approach to improving model performance, i.e., increasing parameterization, has resulted in a wide range of algorithm complexity. Many of these algorithms have remained highly empirical, providing productivity estimates from chlorophyll *a* measurements and a few additional parameters, such as temperature and irradiance (Falkowski 1981, Smith et al. 1982, Balch et al. 1989, Dugdale et al. 1989, and Sathyendranath et al. 1991). An example of these complex empirical formulations, which has met with surprising success in certain regions, is the Ψ model (Falkowski 1981), which has both empirical and analytical properties. Empirically, it has been noted that within certain regions, the relationship between integral production and the product of depth-integrated chlorophyll *a* and time-integrated radiant energy has a remarkably constant slope (Ψ), with an average value of about $0.44 \text{ gC gChl}^{-1} \text{ Ein}^{-1} \text{ m}^{-2}$ †. The constant Ψ model has provided good agreement between estimated and observed primary production in certain oceanic regions (Morel 1978 and Platt 1986), but poor correlation in other regions such as the mid-Atlantic Bight (Campbell and O'Reilly 1988), Southern California Bight (Balch et al. 1989), and South Atlantic Bight (Yoder et al. 1985).

Analytical models incorporate a larger degree of biological and physical detail, placing them at the other end of the parameterized algorithm spectrum. Concepts and mathematical formulations of analytical models are relatively simple, but uncertainties and excessive degrees of freedom in the actual parameterization allow for a number of diverse approaches in model development. It is not possible to present in this paper a comprehensive assessment of the differing approaches to such models (see Bidigare et al. 1992). The general approach of analytical models, however, can be illustrated using two relatively well known bio-optical models, specifically the *Bedford* (Platt et al. 1991) and *LPCM* (Morel 1991) models.

2.2.1.2 "Analytical" Models

The basic procedure for both the *Bedford* and *LPCM* models is to use information on sea-surface chlorophyll concentration to:

- a) First, estimate the vertical distribution of chlorophyll;

† 1 Ein = 1 mole quanta = 1 mole photons

- b) Second, use these modeled chlorophyll profiles and either measurements of surface irradiance or modeled irradiance based on location and date to calculate, from physical principles of light attenuation, the vertical distribution of spectral irradiance; and then
- c) Third, calculate depth-dependent primary production using the modeled chlorophyll normalized photosynthesis (P^B) and irradiance (E) distributions and empirical relationships describing variability in light-limited and light-saturated carbon fixation (i.e., the " P^B vs. E " relationship).

A fundamental difference between the Bedford and LPCM models is that parameters for many of the biological variables in the Bedford model are supplied by seasonally-dependent, provincially specific climatologies based on shipboard measurements, whereas biological variables in the LPCM are parameterized using empirical relationships with surface chlorophyll (C_{sat}). For example, both models describe the vertical distribution of chlorophyll as a Gaussian function of C_{sat} . In the Bedford model, the specific shape of this Gaussian function is provided by a provincially dependent look-up table. In contrast, the LPCM model describes the vertical profile of chlorophyll as a function of various trophic categories defined by C_{sat} , except at high latitudes where a vertically homogeneous distribution is assumed.

The P^B vs. E relationships used in the Bedford and LPCM models have another fundamental difference in that the Bedford model describes photosynthesis as a function of PAR and the LPCM describes it as a function of photosynthetically usable radiation (PUR). Consequently, the LPCM requires additional knowledge about the spectral absorption characteristics of phytoplankton [$\alpha^*(\lambda)$] in order to calculate PUR from PAR, where $\alpha^*(\lambda)$ is empirically parameterized from shipboard measurements. As with chlorophyll distributions, parameterization of the P^B vs. E variables in the Bedford model is provided by provincially defined climatologies. In contrast, the primary variable influencing the P^B vs. E relationship in the LPCM [i.e., K_{PUR} (Morel 1991)] is a temperature-dependent function conforming to the Eppley (1972) description (based on the Arrhenius equation) of the relationship between phytoplankton growth rate and temperature.

Input to the Bedford model include sea-surface chlorophyll concentration, spectral direct and diffuse downwelling irradiance immediately below the sea surface, and the nadir angle of direct radiance immediately below the sea surface. In addition, the geographic location of the input data is required to determine its bio-optical province and thus the associated values for a range of biological variables. Important strengths of the Bedford model are that most of the parameters of the model are readily measurable at sea (a large database already exists) and that the model has been subjected to extensive sensitivity analyses. The principal model assumptions are listed below.

- A. P^B vs. E variables are independent of depth.
- B. Parameters describing the vertical distribution of chlorophyll and the photosynthetic response of phytoplankton are consistent features of a given bio-optical province.
- C. For the description of vertical irradiance distributions:
 - 1) Absorption and scattering coefficients for all marine particulates covary with chlorophyll concentration;
 - 2) The ratio of particulate backscattering to total scattering is constant; and
 - 3) Vertical distribution of downwelling irradiance for diffuse and direct light are independent, downward irradiance can be used in place of scalar irradiance, and there is no augmentation of the diffuse light field by water and particle scattering of the direct irradiance in the water column.

For comparison, input data to the LPCM model include the concentration of chlorophyll and phaeopigments at the sea surface, the spectral downwelling irradiance immediately below the sea surface, SST, mixed layer depth (optional), and the average cosine immediately below the sea surface, although this can be calculated [i.e., (14) of Morel 1991]]. One strength of the LPCM model is that it provides the most accurate and detailed description of the sub-marine light field among the currently available productivity models. Description of photosynthesis in the LPCM model as a function of PUR, rather than PAR, is also advantageous because it permits decomposition of derived parameters into the more fundamental level of irradiance, absorption, and yield. Principal assumptions of the LPCM model include:

1. Absorption spectra and K_{PUR} are independent of depth and the maximum photosynthetic quantum yield is a constant;
2. Vertical chlorophyll distributions are constant for a specific trophic category and vary with time and vary between provinces as a function of C_{sat} ; and
3. Diffuse attenuation, absorption, and scattering coefficients are all functions of chlorophyll alone for Case-1 waters.

2.2.2 Algorithm Parameterization

What input is required by current productivity algorithms and how is this requirement met?

Input data required for the consensus algorithm cannot be specifically identified until the algorithm has been chosen. However, any productivity algorithm used with the SeaWiFS database will be dependent on two types of information:

- 1) That which can be simultaneously measured with, or correlated to, SeaWiFS measurements of water-leaving radiance; and

- 2) That which is based on previously collected oceanographic data, possibly delineated into discrete regions with homogeneous physical, physiological, or optical properties (i.e., biogeographical provinces or climatologies).

The relative importance of the type-1 and type-2 information (above) can vary from algorithm to algorithm. For example, type-1 information required by a purely empirical algorithm may include satellite estimated chlorophyll concentration, latitude, longitude, and date, while the only type-2 requirement is a single regression slope based on an empirical fit to ship-based measurements of primary production. On the other hand, complex analytical algorithms may require simultaneous satellite data such as PAR, chlorophyll, SST, atmospheric aerosol concentration, or cloud-fraction, along with climatological maps of mixed layer depths and photosynthetic parameters, such as P_{\max}^B , α^B , and $KPUR$.

Once a consensus algorithm is chosen, the ancillary data required for calculation of primary production should be archived within the SeaWiFS database. Documentation should be provided for the source of climatological data used by the productivity algorithm. All input data required by the productivity algorithm should be available through NASA, i.e., both type-1 and type-2 information. In addition to chlorophyll, other type-1 data may include SST, which is required for some productivity algorithms and can be obtained from the AVHRR and Along-Track Scanning Radiometer (ATSR) European Remote Sensing Satellite (ERS-1) programs. PAR at the ocean surface and cloud fraction may also be necessary and can be obtained from the International Satellite Cloud Climatology Project (ISCCP). If needed, atmospheric aerosol concentration is available simultaneously with water-leaving radiance from SeaWiFS as a by-product of the data processing. Finally, mixed layer depth (important in some models) is routinely determined by several US agencies and could be made available for the NASA modeling efforts or climatological, e.g., Levitus, data can be used as a first approximation.

Can a consensus be reached on what sea-truth is and, if so, what characteristics can be used to differentiate acceptable from unacceptable data?

One of the primary difficulties in productivity algorithm development is reaching a consensus on the measurement of primary production to be considered *sea truth*. The definition itself of primary production remains elusive, as several definitions may concurrently co-exist according to the time or space scale considered or the particular viewpoint (e.g., plant physiologist, biogeochemist, ecologist, etc.). A methodological protocol can be put forward to more or less adhere to the particular definition of primary production chosen. As a starting point, the OPPWG developed a set of criteria for evaluating the suitability of historical data sets for algorithm testing. The

functional definition of primary production was adopted to be that process measured by the method of radio-labelled carbon uptake during short-term incubations, i.e., the ^{14}C method. It must be recognized that this method does not necessarily represent the best measurement of phytoplankton primary production; it simply represents the largest source of historical data. Indeed, most of the currently available primary production algorithms are based on the results of ^{14}C uptake measurements.

The OPPWG recommended using the 24 hour *in situ* incubation method with 10 levels (see JGOFS protocols). Performance of many current analytical productivity algorithms requires calculation of light harvesting and utilization capability. Therefore, *in situ* ^{14}C productivity should include measurements of the P^B vs. E relationship for samples originating from various depths within the euphotic zone. Results for each P^B vs. E experiment should ideally include the following information.

- A. Spectral distribution of irradiance within an incubator: P^B vs. E experiments using irradiance sources with continuous emission spectra, as in tungsten lamps, should be preferred to those with strong emission peaks, such as fluorescent tubes—if the red enhancement common among lamps with continuous emission spectra has been attenuated, e.g., using blue filters, the resulting spectral composition of the incubation irradiance [source + filter(s)] must be measured.
- B. Measurements of the scalar irradiance gradient will be needed inside the incubation chamber.
- C. Primary production values for several subsaturating incubation irradiance intensities (i.e., light-limitation): this is needed to properly determine the initial slope of the P^B vs. E curve and enough saturating irradiance intensities to clearly define P_{\max} .
- D. The original measured responses of the P^B vs. E experiment prior to any curve fitting: this information is important to evaluate the statistical significance of derived parameters, such as α^B and P_{\max}^B .
- E. Differences between incubation and (*in situ*) temperatures: experimental data from incubations utilizing adjusted temperatures to reproduce *in situ* temperature are preferred.
- F. Spectrally resolved absorption characteristics of the experimental algal population: Kishino (extractive) or numerical decomposition methods should be used (and the details provided) to subtract the non-algal absorption from the total particulate absorption; for absorption spectra measured on filters, the correction method for pathlength amplification (or β effect) must be described.
- G. Time of day during which sampling, incubation, and analysis took place, as P^B vs. E curve characteristics exhibit diurnal changes—it is recommended that daylength and cloud conditions be recorded and regular sampling times be adopted for comparative studies.

- H. *In situ* algal fluorescence profiles are calibrated in terms of chlorophyll.
- I. Detailed pigment composition (photosynthetic, accessory, and photoprotectant) are recorded.

For testing algorithm performance, it is understood that an adequate amount of data is not available that complies to all of the above criteria. However, historical data that are available can be ranked by the number of criteria satisfied and thus, are the best set of test data which can be assembled. It should be noted here that since irradiance is a primary driving force in most productivity models (particular analytical ones), high quality irradiance data, preferably spectrally resolved, should be given equal importance to high quality measurements of biological parameters.

Although the ^{14}C method is the most common method of measuring phytoplankton primary production, there are many problems associated with the interpretation of ^{14}C data. Therefore, priority should also be given to developing databases of alternative primary production measures. For example, relationships have been developed between gross photosynthesis and variable fluorescence parameters [such as from the Fast Repetition Rate (FRR) fluorometer]. A substantial amount of FRR data is already available and may provide insights into algal physiology, which allow fundamental parameters of photosynthesis to be better quantified. Moreover, these methods provide nondestructive, rapid measurements of photosynthetic parameters and thus, allow estimates of primary production over a continuous vertical profile without the artifacts associated with prolonged incubations.

2.2.3 Algorithm Testing and Validation

How can algorithm performance be tested objectively?

Before any statement regarding algorithm validation is made, recall that a primary goal of a consensus productivity algorithm is to observe variability in oceanic primary production occurring on interannual-to-decadal time scales and regional-to-global space scales. It is impossible to observe variability at these scales by any means other than by satellite. Validation of a productivity algorithm seeks to establish whether or not it is possible to observe large-scale variability even with satellites. The goal to "observe variability" is more specifically the detection of change or trends, thus requiring precision rather than accuracy. Some level of variability will exist in satellite productivity estimates regardless of whether true climate induced change is occurring. Thus, the fundamental question is, "What level of precision is required of the consensus algorithm to enable detection of a true trend in productivity within the time frame of interest?"

There are two error sources for large-scale primary production estimates:

- 1) Statistical errors resulting from undersampling, because estimates are based on finite data sets with limited spatial and temporal coverage; and
- 2) Methodological errors resulting from inaccuracies in observations made at a particular location.

Estimates of global productivity based on *in situ* measurements alone are critically limited by large undersampling errors. Satellite derived estimates of global productivity have the advantage of much greater spatial and temporal coverage. Unfortunately, satellite estimates are fundamentally limited to those properties amenable to remote sensing (C_{sat} , incident solar radiation, SST, etc.), which alone do not sufficiently determine primary productivity without large methodological errors.

Most analyses of primary productivity algorithms have focused strictly on methodological errors in satellite derived estimates by comparison with *in situ* measurements (e.g., Balch et al. 1992); however, *in situ* measurements also contain methodological errors. Methodological and statistical errors associated with both *in situ* measurements of primary production, as well as satellite data and usage, must therefore be considered.

2.2.3.1 Methodological Error

In situ methods: The ^{14}C method has evolved over several decades and, although many investigators follow somewhat similar procedures, no standard protocol is internationally implemented, even within a single program such as JGOFS. The ^{14}C technique requires several steps, including:

- a) Collecting uncontaminated seawater samples;
- b) Spiking samples with ^{14}C -bicarbonate that is not contaminated with trace metals and other potentially toxic substances;
- c) Conducting experiments under conditions that do not kill or harm the plankton;
- d) Collecting dissolved and particulate phases of ^{14}C -labelled organic matter;
- e) Measuring the ^{14}C activity; and
- f) Extrapolating experimental results back to natural conditions.

Most steps in this list include unknown measurement errors and biases, which are rarely specified.

Satellite method: Validation of SeaWiFS-derived primary production estimates is the process of comparing calculated productivity with *in situ* measurements. Both results contain many known and unknown sources of error and investigator-specific bias. It is generally assumed that methodological errors in *in situ* measurements are small compared with those of satellite-based algorithms. Based on this assumption, it has been shown that primary productivity algorithms can, at best, account for only 50–60% of the total variance in measured daily productivity (e.g.,

Balch et al. 1992). This error estimate is based on algorithms tested using *in situ* data only. When the added error incurred by using satellite data as input (e.g., inaccurate C_{sat} estimates) is taken into account, methodological errors associated with satellite algorithms will be larger.

2.2.3.2 Statistical Errors

In situ methods: Koblenz-Mishke et al. (1970) estimated global oceanic primary production based entirely on *in situ* measurements. They divided the ocean into biogeographic regions (oligotrophic, transitional, etc.), assigned a characteristic average daily productivity to each region (in units of $\text{gC m}^{-2} \text{d}^{-1}$), and multiplied daily production by regional area and 365 d yr^{-1} to arrive at total annual production (in units of tC y^{-1}). Regions were defined by topography or geography and boundaries (hence, areas) were fixed. Uncertainties associated with such estimates result from an uncertainty in the regional mean productivity values, which are based on relatively small data sets and thus subject to large, but unknown, statistical undersampling errors.

Satellite method: Spatial and temporal coverage by satellite measurements will always far exceed those of ship-based measurements. Thus, it is generally believed that satellite estimates will have smaller statistical errors, but this has not been quantified (although see Sathyendranath et al. 1991). Precision can be achieved in satellite estimates of large-scale primary production, despite large methodological errors, if the productivity algorithm's methodological errors are random and unbiased. In other words, the errors associated with point estimates of primary productivity derived from satellite data should exhibit no systematic geographical or temporal pattern relative to *in situ* measurements, provided equal error exists between biogeographical provinces.

Primary production is not a geophysical measurement, and therefore, has to be validated differently than SST, wind velocity, sea level, and other satellite-derived ocean properties. Large methodological errors may be admissible as long as they are unbiased and show no systematic patterns, either geographically or seasonally. If provincial algorithms are adopted, validation will require testing whether or not classification algorithms accurately predict the boundaries of biogeographical provinces. For validating complicated primary production algorithms, there are two distinct levels of testing. The first step is to compare model output of primary production (e.g., as $\text{gC m}^{-2} \text{d}$) to *in situ* measurements. This step in the validation process does not determine accuracy, but gives a measure of consistency among the various methods. The second step is to validate the individual components of a primary production algorithm. For example, how do the values chosen for the chlorophyll field, physiological parameters (e.g., P_{max}), and incident solar irradiance compare with measurements? This is an important step, since accuracy can be specified

for at least some of the components and, at least in principle, an estimate of the total error can be determined. More importantly, this second validation step will reveal why primary production algorithms yield results that differ from *in situ* measurements and thereby can lead to improved algorithms and provide an objective way to set priorities for validation efforts.

At what level should the consensus productivity algorithm be available to investigators using SeaWiFS data, and what information should be archived?

One of the motivations for developing a consensus algorithm is to allow easy access to primary production estimates for investigators using SeaWiFS ocean color data. It must be stressed that, like algorithms for estimating chlorophyll concentration, the consensus algorithm implemented as a standard SeaWiFS product represents the state of the science at the time of implementation and will be iteratively improved as advances are made in understanding the relationship between phytoplankton biomass and photosynthesis. It is the responsibility of the investigator to be aware of the uncertainty in the productivity estimates. Thus, the consensus algorithm must be accompanied by:

- 1) Documentation of the algorithm source (including how constants and parameter values were chosen);
- 2) A statistical summary of comparisons used to identify the algorithm;
- 3) Access to, and information on, the sources of *in situ* measurements used for algorithm validation; and
- 4) A list of additional published algorithms which may provide different estimates of primary production.

Estimated standard errors for calculated productivity should be clearly stated as both a percentage error and an absolute difference when compared with *in situ* measurements. Statistical methods and *in situ* data sets used in estimating this error should be clearly documented.

2.3 CONCLUDING REMARKS

The goal of the OPPWG is to systematically develop well-documented consensus models of primary production in the sea. It is crucially important that NASA maintain a very long-term perspective on global change research. A century from now, scientists must be able to compare satellite chlorophyll maps from CZCS and SeaWiFS with those of that time, with reasonable confidence that:

- a) The radiance values are correct;
- b) The algorithms used for atmospheric corrections and chlorophyll concentrations were uniform from mission to mission; and
- c) If there is a change in phytoplankton biomass, it is not due to instrument degradation or algorithm improvement.

It is not as critical to know the absolute value of the biological state variables as their changes and the reasons for their changes. To this end, the approach described herein to develop a consensus production model based on a traceable data set, will allow objective comparisons of decadal changes in primary production in the world ocean. Even if the models are imperfect, as they are bound to be, the scientific community should attempt to develop some compromises in production models that provide an understanding of the causes of true changes in phytoplankton biomass and production from the noise of investigator-dependent model parameterization. It is time that production models be systematically implemented using global data sets through cooperative involvement.

APPENDICES

- A. Participants in the OPPWG
- B. What is Photosynthesis?
- C. What is Primary Production?
- D. The Atmospheric CO₂ and O₂ Cycles

Appendix A

Participants in the OPPWG

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Appendix B

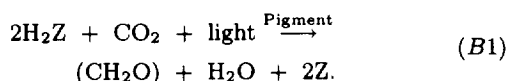
What is Photosynthesis?

Two astrophysically detectable criteria for detecting life on other planets are the presence of liquid water and gaseous oxygen. These two criteria are selected because, on Earth, they are causally related. The Earth's atmospheric oxygen is derived from the photochemical splitting of water through the biologically mediated process of photosynthesis. There is no other known biological process that leads to the evolution of gaseous O₂. Oxygenic photosynthesis evolved in the Archean Oceans, approximately 3.5 billion years before present, which fundamentally changed the chemistry of Earth (Kasting 1993). Over the following 3 billion years, oceanic photosynthesis was the driver of the major biogeochemical cycles on Earth. The affected cycles include not only oxygen, but carbon, nitrogen, phosphorus, silicate, sulfur, and myriad trace elements (Holland 1984 and Berner 1993).

On the most fundamental level, a major goal of the MTPE is to understand the factors controlling global oxygenic photosynthesis on both ecological and geological time scales. Such an effort is critical to the MTPE mandate to develop observational tools to assess the effects of potential anthropogenic activities on Earth's environment.

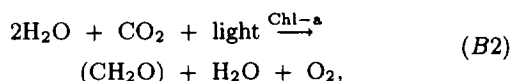
The biological economy of Earth is based on the chemistry of carbon. The vast majority of carbon on Earth is in an oxidized, inorganic form [i.e., combined with molecular oxygen and in the form of carbon dioxide (CO₂), or its hydrated or ionic equivalents, namely bicarbonate (HCO₃⁻) and carbonate (CO₃²⁻)]. The inorganic forms of carbon are interconvertible and thermodynamically stable, contain no biologically usable energy, and cannot be used directly to form organic molecules without undergoing a chemical or biochemical reaction. In order to extract energy from inorganic carbon, or to use the element to build organic molecules, carbon must be chemically reduced or fixed. This process requires an investment in free energy. There are only a small amount of biological mechanisms extant for the reduction of inorganic carbon and, on a global basis, photosynthesis is by far the most familiar, most important, and most extensively studied.

Photosynthesis is a coupled oxidation-reduction reaction of the general form:



Note that in this representation, light is specified as a substrate for photosynthesis such that the energy of the absorbed light is stored in the photosynthetic products. The quantum yield of photosynthesis can, therefore, be described as the ratio CH₂O:light-absorbed.

All photosynthetic bacteria, with the important exceptions of cyanobacteria and prochlorophytes, are obligate anaerobes and incapable of evolving oxygen. In these organisms, the substrate, Z (B1), would be an atom of sulfur, for example, and the pigments (B1) would be bacterial chlorophylls (Blankenship 1992). All other photosynthetic organisms are oxygenic, including cyanobacteria, prochlorophytes, eukaryotic algae, and higher plants; thus, (B1) can be modified for these organisms to:



where Chl-a is the ubiquitous plant pigment, chlorophyll a. The redox midpoint potential for the oxidation of water is 1.23 eV³. To catalyze such a high energy oxidation, a special chlorophyll a becomes transiently photochemically ionized in the so-called photosynthetic reaction centers. This ionization creates the strongest biologically produced redox couple known.

Globally, photosynthetic evolution of oxygen is approximately balanced by the amount of inorganic carbon fixed. Likewise, oxygen is consumed during respiratory oxidation of organic carbon compounds. Respiration provides free energy for all life on Earth. On geological time scales, photosynthetic carbon fixation has exceeded the respiratory oxidation of organic carbon. In the Archean or early Proterozoic eons, the imbalance between these two processes permitted O₂ to accumulate in Earth's atmosphere and simultaneously resulted in a drawdown of atmospheric CO₂. The imbalance has continued through the Phanerozoic epoch to the present, leading to the organic carbon deposits that presently fuel anthropogenic industries (see Fig. 1).

Appendix C

What is Primary Production?

The parameter estimated by productivity models varies according to the time interval of model integration, and the distinction between these parameters, is critical for understanding the output of a standard productivity algorithm and for the correct application of this output.

Gross photosynthesis, P_G , is defined as the number of electrons photochemically produced from the splitting of water. Net photosynthesis, P_n , is defined as:

$$P_n = P_G - R_l, \quad (\text{C1})$$

where R_l is all the losses of fixed carbon due to respiratory processes of the photosynthetic organism in the light; thus, by definition, photosynthesis can occur only in the light. There are also respiratory losses in the dark, i.e., at night. Primary productivity, PP , includes these dark losses and can be described by the integral:

$$PP = \int (P_n - R_d) dt, \quad (\text{C2})$$

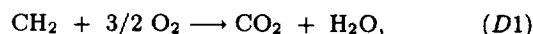
where R_d is dark respiration by the photosynthetic organism. Primary productivity has dimensions of carbon fixed, or oxygen evolved, per unit area and per unit of time; thus, it is a rate. Total primary productivity, is the integrated water column primary productivity.

Export primary production is that fraction of the total primary production that sinks to the ocean interior. In contrast, new primary production is that fraction of the total primary production which is supported by a flux of nutrients external to the euphotic zone. The fraction, f , is the ratio of new primary production to total primary production. Sources of such nutrients include vertical fluxes from the ocean interior, biological nitrogen fixation, atmospheric deposition, and lateral fluxes from terrestrial runoff. In a steady state approximation, export production equals new production.

Appendix D

The Atmospheric CO₂ and O₂ Cycles

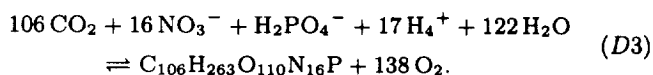
Changes in atmospheric O₂ and CO₂ are linked by reactions involving the formation and destruction of organic matter. The dominant reactions include fossil-fuel burning



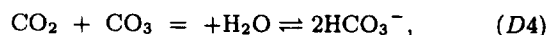
and photosynthesis and respiration of terrestrial biota



where CH₂ and CH₂O schematically represent the chemical composition of fossil-fuel and terrestrial organic material, respectively. Changes in dissolved O₂ and CO₂ in the ocean are similarly linked by photosynthesis and respiration of marine biota



The carbon cycle in seawater is additionally influenced by reactions of the carbon system in seawater, such as:



which, together with photosynthesis, are the dominant reactions mediating the uptake of excess anthropogenic CO₂ by the ocean. This suite of organic and inorganic reactions, combined with exchanges across the air-sea interface driven by disequilibria between the air and sea, are the dominant controls on atmospheric and oceanic CO₂ and O₂ abundance on time scales shorter than many thousands of years.

Observed trends in atmospheric O₂ abundance can place constraints on the large-scale fluxes of CO₂ between the atmosphere and ocean. For example, the decrease in atmospheric O₂ abundance, corrected for reaction stoichiometry and the increase in atmospheric CO₂, can determine the rates at which excess CO₂ is removed from the atmosphere by physical dissolu-

tion in the ocean. Another constraint is based on the seasonal cycles in atmospheric O₂. These cycles are caused partly by exchanges with terrestrial biota and partly by exchanges of O₂ between the air and sea. The latter are a reflection of seasonal variations in the strength of the biological pump in the ocean. Photosynthesis rates in the upper ocean tend to be maximal in the spring and summer under conditions when surface waters have ample nutrients and when vertical mixing is suppressed by the stable stratification in the water column. A considerable fraction of the O₂ produced at this time escapes into the atmosphere. Comparable amounts of O₂ are removed from the atmosphere in the autumn and winter when surface cooling causes oxygen-depleted waters to be mixed from the deep ocean interior up to the surface. The air-sea O₂ fluxes associated with this seasonal cycle in the biological pump are closely linked to the rates at which organic material is produced and exported from the euphotic zone.

The seasonal cycles in photosynthesis and mixing in the ocean also lead to changes in the CO₂ partial pressure in seawater, which in turn lead to changes in CO₂ in the atmosphere. Changes in atmospheric CO₂ because of these cycles are much smaller than changes in atmospheric O₂, however, because of the buffering of the carbon system in seawater by inorganic reactions. The variations in atmospheric CO₂ caused by seasonal air-sea exchange are largely masked by much larger exchanges with terrestrial biota. In contrast, variations in O₂ cycles arising from seasonal exchanges are generally larger than variations caused by terrestrial biota. Thus, the variations in O₂ place more powerful constraints on variations in the marine biological pump than do the corresponding variations in CO₂.

Variations in the strength of the biological pump from year to year may be manifested in changes in the amplitude of the seasonal cycle of O₂ in the atmosphere. Because of rapid mixing, the atmosphere acts as a natural integrator for large-scale processes, so changes seen in background air are a measure of large-scale processes. Changes in the strength of the biological pump detected in atmospheric O₂ would complement changes seen through satellite measures of ocean color. Satellite data would determine with more detail the spatial patterns of variations, while O₂ data would place constraints on the large-scale perturbation due to chemical fluxes.

GLOSSARY

AM-1 Morning crossing of MODIS
 ATBD Algorithm Theoretical Basis Document
 ATSR Along-Track Scanning Radiometer
 AVHRR Advanced Very High Resolution Radiometer
 BATS Bermuda Atlantic Time Series
 BPM Bedford Production Model
 CZCS Coastal Zone Color Scanner
 DAAC Distributed Active Archive Center
 DIM Depth Integrated Model
 DIN Dissolved Inorganic Nitrogen
 DIP Dissolved Inorganic Phosphate
 DOE Department of Energy (US)
 E&P Eppley and Peterson (compilation)
 ECS EOSDIS Core System
 EOS Earth Observing System
 EOSDIS EOS Data Information System
 ERS-1 European Remote Sensing Satellite
 FRR Fast Repetition Rate (fluorometer)
 FTP File Transfer Protocol
 GAC Global Area Coverage
 GISS Goddard Institute for Space Studies
 GSFC Goddard Space Flight Center
 HOTS Hawaii Ocean Time Series
 IGBP International Geosphere-Biosphere Programme
 ISCCP International Satellite Cloud Climatology Project
 JGOFS Joint Global Ocean Flux Study
 LANDSAT Land Resources Satellite
 LPCM Laboratoire de Physique et Chimie Marines
 MERIS Medium Resolution Imaging Spectrometer
 MODIS Moderate Resolution Imaging Spectroradiometer
 MTPE Mission to Planet Earth
 Myr Millions of Years
 NASA National Aeronautics and Space Administration
 NSF National Science Foundation
 OPPWG Ocean Primary Productivity Working Group
 PAR Photosynthetically Available Radiation
 PPARR-1 First Primary Productivity Algorithm Round-Robin (October 1995)
 PPARR-2 Second Primary Productivity Algorithm Round-Robin (August 1997)
 PPARR-3 Third Primary Productivity Algorithm Round-Robin (being planned)
 PGS Product Generation System
 PM-1 Afternoon crossing of MODIS
 PUR Photosynthetically Usable Radiation
 rms root mean squared
 SCF Science Computing Facility
 SeaWiFS Sea-viewing Wide Field-of-view Sensor
 SIMBIOS Sensor Intercomparison and Merger for Biological and Interdisciplinary Oceanic Studies
 SST Sea Surface Temperature
 TLCF Team Leader Computing Facility
 TIM Time Integrated Model

USDA United States Department of Agriculture

VGPM Vertically Generalized Production Model

WIM Wavelength Integrated Model

WRM Wavelength Resolved Model

SYMBOLS

C_K Average chlorophyll *a* concentration within the first optical depth (mgChl m^{-3}).
 C_{sat} Satellite-based surface chlorophyll concentration (mgChl m^{-3}).
 $(\text{CO}_2)_{\text{GLOB}}$ Global CO_2 concentration in parts per million.
 d_{PC} Daily depth-integrated primary production ($\text{mgC m}^{-2} \text{d}^{-1}$).
 DL Day length.
 f The ratio of new primary production to total primary production.
 $KPUR$ A temperature-dependent variable in the productivity model of Morel (1991) that defines the shape of the photosynthesis-irradiance relationship.
 $(\text{O}_2/\text{N}_2)_{\text{ref}}$ The referenced amount of O_2/N_2 .
 $(\text{O}_2/\text{N}_2)_{\text{samp}}$ The sampled amount of O_2/N_2 .
 $P^b(z)$ Chlorophyll-specific photosynthetic rate at depth z .
 P_{opt}^b Maximum chlorophyll-specific carbon fixation rate within a water column.
 P^B Chlorophyll normalized photosynthesis.
 P_{max}^B P_{max} normalized to chlorophyll concentration.
 P_G Gross photosynthesis is defined as the number of electrons photochemically produced from the splitting of water.
 P_{max} Light saturated rate of photosynthetic carbon fixation.
 P_n Net photosynthesis is defined as $P_G - R_l$.
 P_{PC} Annual average phytoplankton particulate organic carbon production ($\text{gC m}^{-2} \text{yr}^{-1}$).
 P_T Depth-integrated primary production.
 PP Primary productivity.
 R Phytoplankton respiration.
 R_d Dark respiration by the photosynthetic organism.
 R_l All the losses of fixed carbon due to respiratory processes of the photosynthetic organism in the light.
 t Time.
 T^o Levitus climatological median upper ocean temperature (18.1°C) as computed by Antoine et al. (1996).
 z Depth.
 z_{eu} Depth of the euphotic zone.
 Z A substrate.
 * Normalization-to-chlorophyll concentration.
 α Light-limited slope of the photosynthesis-irradiance relationship.
 $\alpha^*(\lambda)$ Chlorophyll-specific, spectral absorption coefficient for phytoplankton.
 α^B Chlorophyll normalized α .
 β The correction method for pathlength amplification.
 $\delta(\text{O}_2:\text{N}_2)_{\text{GLOB}}$ The changes in the global $\text{O}_2:\text{N}_2$.
 ΔT Changes in temperature.

λ Wavelength.

Π Depth-integrated primary production.

ΣPP Classification system for primary productivity models based on implicit levels of integration.

Φ A photoadaptive variable which is a chlorophyll-specific quantum yield for absorbed PAR.

φ A photoadaptive variable which is a chlorophyll-specific quantum yield for available PAR.

Ψ Ratio of depth-integrated primary production to the product of depth-integrated chlorophyll *a* and time-integrated radiant energy [$\text{gC}(\text{gChl})^{-1} \text{Ein}^{-1} \text{m}^{-2}$].

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